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DEMOGRAPHY OF TUNDRA AND TAIGA POPULATIONS OF *CLETHRIONOMYS RUTILUS*

by

© ARTHUR MELVIN MARTELL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Demography of tundra and taiga populations of *Clethrionomys rutilus*" submitted by Arthur Melvin Martell in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Tundra and taiga populations of the northern red-backed vole, *Clethrionomys rutilus*, were studied in the Northwest Territories from 1971 to 1973 primarily by means of dead-trapping and autopsies. Taiga study sites were within 6 km southeast of Inuvik (68°00'N; 133°43'W) and primary tundra study sites were within 15 km of Tununuk Pt. (69°00'N; 134°40'W), approximately 80 km northwest of Inuvik.

Age of animals was determined by stage of development of the second upper molar. Reproduction; body and skull size; adrenal, kidney, and interscapular brown adipose tissue weights; and wounding were analyzed in relation to changes in relative numbers and environmental conditions. Animals were shorter, but not lighter, in the taiga in 1971 than in other years in the taiga or on the tundra; this may have been related to the high population density in 1971. Adrenal weights did not reflect changes in relative population density, and kidney and interscapular brown adipose tissue weights generally reflected only annual changes in environmental conditions. Incidence of wounding was higher in the taiga in 1971 than in 1972 or 1973; this was related to the high population density in 1971. Incidence of wounding in late-born young-of-the-year was generally higher on the tundra than in the taiga. It was hypothesized that this was due to intensive intraspecific competition for the restricted suitable overwintering habitat on the tundra.

Taiga population indices (number caught/100 trap nights dead trapping) at the beginning of summer decreased from 1971 (4.4) to 1972 (1.9) and 1973 (1.2), but late summer indices were higher in 1971 (7.7)

and 1973 (6.8+) than in 1972 (4.1). Tundra population indices were lower than those in the taiga and were probably similar each year at the beginning of summer (about 0.5). Late summer indices were likely similar in 1971 and 1972 (6.5) but were lower in 1973 (2.1).

Changes in population size were caused primarily by differences in overwintering mortality and annual production. Variations in overwintering mortality (55-95%) were attributed to differences between years and areas in environmental conditions during fall critical period, winter, and spring critical period. Variations in summer production were caused by variations in the proportion of first-litter young breeding in the year of their birth (45-77% of females; 2-38% of males). The proportion of first-litter young breeding appeared to be inversely related to population density at the beginning of summer.

The populations studied did not offer impressive evidence of being cyclic. It was hypothesized that the taiga population was regulated by density-dependent regulation of the proportion of first-litter young breeding in the year of their birth; while the tundra population was controlled by density-independent overwintering survival. Extrinsic factors, therefore, played a greater role than intrinsic factors in control/regulation of the tundra population; while the roles were reversed in the taiga.

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INTRODUCTION

Elton (1924) first clearly pointed out the marked fluctuations in animal populations, particularly those in northern areas. Since that time interest in population dynamics has increased (see Warren 1958, Boer and Gradwell 1971) and many theories of population regulation have been advanced (see Bakker 1964, Clark *et al.* 1967). Population fluctuations have often been particularly marked in small rodents (Elton 1942) in regions where snow is an integral part of their environment (Formozov 1946).

Fuller (1967) reviewed some characteristics of the northern environment and stated that he believed it was some of these features which play an essential role in controlling the numbers of northern animals. He suggested that there are two critical periods in the year for small mammals. The first had previously been suggested by Pruitt (1957) and is the time of changeover from summer to winter conditions. The type of fall, Fuller suggested, would affect rodent populations both directly through mortality and indirectly through the degree of preservation of the food supply. The second critical period occurs during the changeover from winter to summer conditions. This spring critical period, Fuller noted, had previously been implicated by Soviet workers at least since Dunaeva (1948). The spring critical period could affect small mammals both through mortality and by controlling the timing of the onset of breeding. Fuller *et al.* (1969) also hypothesized that winter mortality might control the numbers of small mammals in regions with long snowy winters but his study (Fuller 1969) in the taiga*

*In this thesis the term taiga will be used for the northern coniferous (boreal) forest (Hoffmann 1958).

provided no support for this hypothesis. However, the study did indicate the importance of the spring critical period and suggested that it acted "not through altering mortality, but through advancing or retarding breeding and hence altering recruitment." Recent studies have indicated the importance of the spring critical period (Fuller *et al.* 1975b) and of the fall critical period and winter conditions (MacLean *et al.* 1974, Pitelka 1973) to lemmings in tundra areas.

Snow conditions vary drastically between soft, relatively even snow in the taiga and dense, unevenly distributed snow on the tundra (Formozov 1946, Pruitt 1965, 1970). Taiga snow generally provides better insulation for subnivean mammals than tundra snow.

The northern red-backed vole, or red vole, *Clethrionomys rutilus* (Pallas), occurs throughout the Eurasian taiga, the species' northern boundary coinciding approximately with the treeline, but with some intrusions into the tundra (Ognev 1950). In northwestern North America, however, it is common on the mainland tundra as well as in the taiga (Bee and Hall 1956, Manning 1956). Because the species spread into most of its North American range since the end of the last glaciation (Macpherson 1965), *C. rutilus* can be considered to be primarily a taiga species which only relatively recently has exploited tundra habitats to any extent (*cf.* Schwartz 1963).

Taiga populations of *C. rutilus* have been studied in the Soviet Union (Koshkina 1957, 1965, 1966b, 1967a,b, 1974a; Krivosheev 1961; Popov 1964; Shtil'mark 1965 and others) and in North America (Fuller 1969; Fuller *et al.* 1969; Sealander 1966, 1967, 1969, 1972; Sealander and Bickerstaff 1967; Whitney 1973 and others) but tundra populations have received little attention (Bee and Hall 1956, Manning 1956, Mayo

1963, Pruitt 1966) and no comparative work has been done.

The uplands east of the Mackenzie Delta, Northwest Territories, include taiga and tundra areas in close proximity due to a narrow transition zone. The macroclimate, microtopography, and ground cover and shrub-layer vegetation are quite similar but, as mentioned previously, snow cover is markedly different. This then presents an area where a comparative study of taiga and tundra populations might provide a basis for testing Fuller's hypothesis on the role of fall and spring critical periods and winter conditions on small rodent populations.

One would predict that the effect of adverse fall, winter, and spring conditions would be more pronounced on the tundra than in the taiga and that this might be apparent in the mortality rates, timing and intensity of reproduction, and general condition of the two populations. This study was designed to monitor simultaneously both tundra and taiga populations of *C. rutilus* to see if such differences were apparent and if they were related to differences in snow cover and environmental conditions.

STUDY AREAS

The taiga study sites lie within 6 km southeast of Inuvik (68°00'N; 133°43'W) and the tundra study sites lie within 15 km of Tununuk Pt. (69°00'N; 134°40'W), approximately 80 km northwest of Inuvik (Fig. 1). In 1971, a tundra site 11 km south of Tuktoyaktuk (69°27'N; 133°02'W) was also trapped.

The Tununuk study area is in the Tununuk Low Hills Section (IIIa) of the Pleistocene Coastlands Physiographic Region of Mackay (1963).

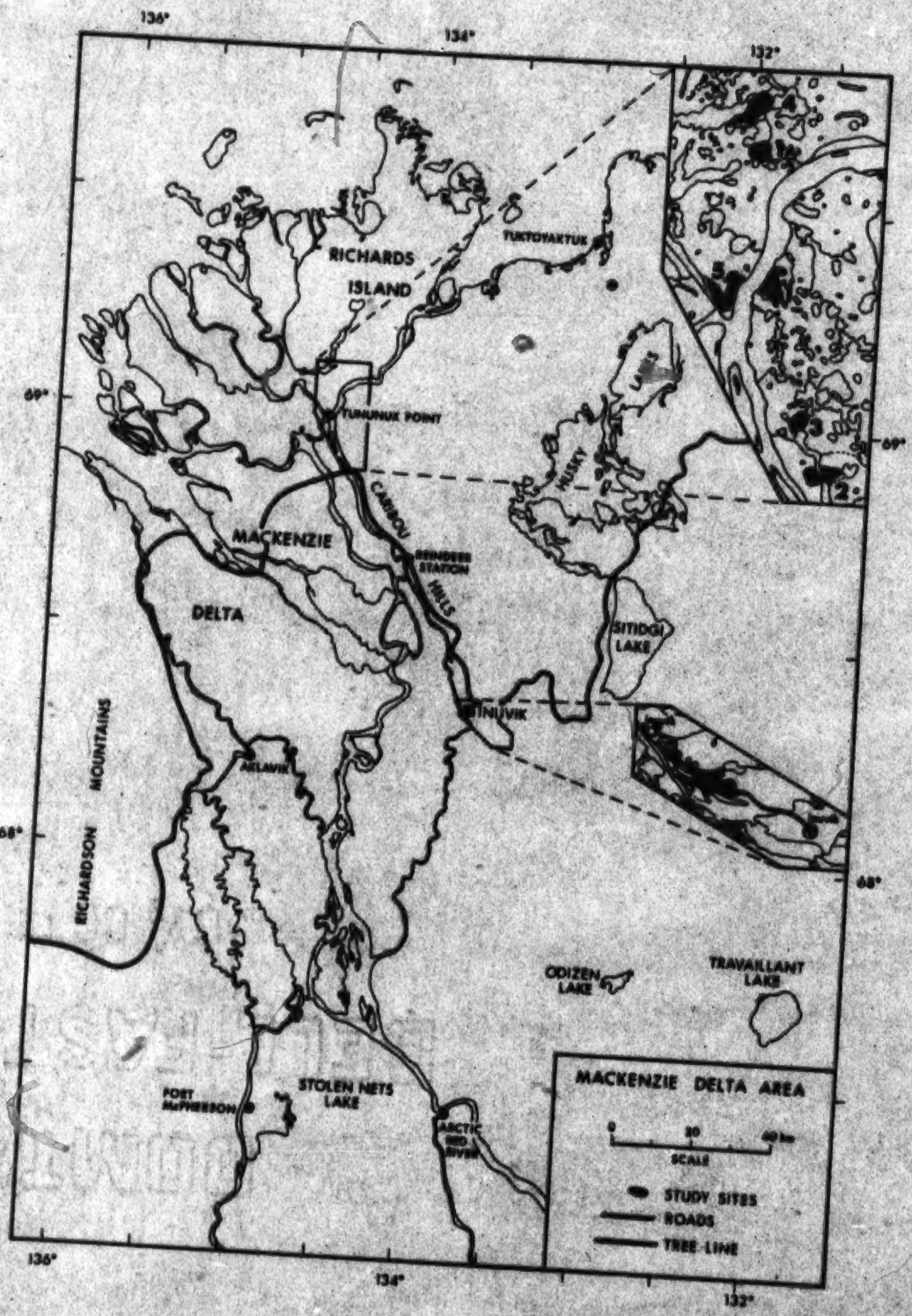

Figure 1. Map of Mackenzie Delta area showing location of study sites.

This area is characterized by gently rolling hills up to 61 m in height. The vegetation of the area has been described by Cody (1965), Corns (1972, 1974) and Lambert (1972). At the primary Tununuk study sites the dead-trap stations were classified as to habitat type according to Corns (1972, 1974) with the modification that each of the heath classes was divided according to presence or absence of *Alnus crispa*: Sedge Heath became Sedge Heath and Sedge-Alder Heath (Table 1). The study sites were dominated by dwarf shrub-heath communities characterized by a shrub layer of *Betula glandulosa*, *Salix glauca*, and *Alnus crispa*. Associated with these shrubs are many heath species such as *Ledum palustre*, *Empetrum nigrum*, *Rhododendron lapponicum*, *Arctostaphylos rubra*, *A. alpina*, *Vaccinium uliginosum*, and *V. vitis-idaea*. Also associated with these communities are species such as *Carex lugens*, *Lupinus arcticus*, *Rubus chamaemorus*, *Pedicularis lanata*, and *Petasites frigidus*, as well as mosses and lichens. In moister locations *Carex lugens* and varying amounts of *Eriophorum vaginatum* dominate the ground cover.

The Inuvik study area is in the Campbell Lake Hills Physiographic Region (Va) of Mackay (1963). This is a rocky and hilly area with a thin veneer of glacial till. The forests are in the Open Woodland Zone of the Boreal Forest (Hare and Ritchie 1972) and in the White Spruce-Black Spruce-Lichen Region (I) of Zoltai and Pettapiece (1973). The area has been burned repeatedly and all study sites are in approximately 80-120 year old burns. Reestablishment of the forest takes about 150 years on dryer sites and may take hundreds of years on moister sites (Zoltai and Pettapiece 1973). According to Strang (1973) the absence of fires would lead to an almost tundra-like condition in the area. While there are no quantitative studies on the forests of the study

Table 1. Percentage of dead-trap stations in each habitat type for the Tununuk study area. Number of stations classified in brackets.

Habitat Type (modified from Corns 1972, 1974)	Study Sites 1 [374]	2 [800]	3 [1000]	4 [900]	5 [500]
Tall Shrub-Herb Type	1.1	0.2	0.2	0.2	0.4
Dwarf Shrub-Heath Type	89.8	79.9	62.2	73.5	77.6
Birch-Alder Heath	(71.6)	(19.6)	(20.8)	(14.9)	(56.8)
Birch Heath, Birch-Willow Heath, & Willow Heath	(18.2)	(60.3)	(41.4)	(58.6)	(20.8)
Herb-Dwarf Shrub-Heath Type	9.1	19.8	37.6	26.2	22.0
Sedge-Alder Heath & Sedge-Cottongrass-Alder Heath			(23.0)	(11.3)	(14.0)
Sedge Heath & Sedge-Cottongrass Heath	(9.1)	(14.2)	(7.1)	(14.9)	(8.0)
Lichen Heath		(5.6)			
Lichen-Polygon Heath			(7.5)		

area, similar forests have been examined in the mountains west of the Mackenzie Delta (Wein 1971, Hettinger *et al.* 1973).

The successional forests of the study area fall into two main types: paper birch-white spruce forests on relatively dry south or southwest facing slopes, and black spruce forests on other exposures. Willow associations occupy lowlying drainage channels but these were not trapped extensively. The paper birch-white spruce forest is dominated by *Betula papyrifera humilis* with a small mixture of *Picea glauca*. *Salix* spp. is sparse in some stands and very dense in others. Low shrubs, *Betula glandulosa* and *Ledum palustre*, are not common and ground cover tends to be sparse. The major ground cover species are *Vaccinium vitis-idaea*, *Empetrum nigrum*, *Ribes triste*, *Lupinus arcticus*, *Pyrola secunda*, and *Rosa acicularis*. Mosses and lichens are common but not abundant. The black spruce forest is characterized by *Picea mariana* and varying amounts of *Salix* spp. There is a dense shrub layer of *Betula glandulosa* and *Ledum palustre*. The major associates of the community are *Rosa acicularis*, *Petasites frigidus*, *Calamagrostis canadensis*, *Rubus chamaemorus*, and *Vaccinium vitis-idaea*. Some other species present are *Pyrola grandiflora*, *Eriophorum vaginatum*, *Empetrum nigrum*, and *Vaccinium uliginosum*. There is also a dense ground cover of mosses and lichens.

Lambert (1972) noted that, on the uplands east of the Mackenzie Delta, the dominant plant species appear almost everywhere in the tundra and forest communities without regard to landform. These are, he noted, *Betula glandulosa*, *Vaccinium vitis-idaea*, *Ledum palustre*, *Empetrum nigrum*, and *Arctostaphylos rubra*. Throughout both the taiga and tundra, earth hummocks of 70-170 cm in diameter and up to 35 cm high are common elements of the ground surface (Mackay 1963). Therefore,

although there is a marked shift in plant communities from taiga to tundra, the microtopography and the plants with which small mammals are closely associated are essentially the same.

CLIMATE

The seasons will be considered in terms of snow on the assumption that it is the single most important climatic factor to northern small mammals. Winter, therefore, is the season of persistent snow cover, and hence relatively stable subnivean conditions; summer is the season without a persistent snow cover. There is a period of active snow melt in late May or early June marking the changeover from winter to summer conditions and an ephemeral period in late September or early October preceding the establishment of a persistent snow cover and marking the changeover from summer to winter conditions. This latter period is often characterized by frequent light snowfall and rapid melting. These times of changeover are the spring and fall critical periods proposed for northern small mammals (Dunaeva 1948, Fuller 1967, Pruitt 1957). Spring and autumn are of short duration; therefore, small mammals in the study areas experience, in effect, only two seasons: a four-month summer and an eight-month winter.

Since 1957 there has been a weather station operating at the Inuvik airport, approximately 7 km southeast of the taiga study area, and at Tuktoyaktuk, approximately 80 km northeast of the tundra study area. A weather station operated at Tununuk Pt., the centre of the tundra study area, from 1957 to 1963. Normal* values for Inuvik and Tuktoyaktuk are

*'Normal' refers to those values published as such by Environment Canada, Atmospheric Environment Service. Conversions were made from English to metric units.

more representative than those at Tununuk Pt. due to the longer record, a point to be kept in mind when comparisons are made.

Normal mean monthly temperatures for Inuvik, Tununuk Pt., and Tuktoyaktuk (Fig. 2A) are similar during the period of changeover from summer to winter conditions (September-October). During most of the winter (November-April) temperatures at Tununuk Pt. and Tuktoyaktuk are similar to each other, but Inuvik has lower mean minimum temperatures November to February and higher mean maximum temperatures in March and April. At the time of changeover from winter to summer conditions (May-June) Inuvik is warmest, both in mean minimum and mean maximum temperatures, and Tuktoyaktuk is coldest. All three areas are similar in July and August, although Inuvik has somewhat higher mean maximum temperatures.

All three stations show similar amounts of rainfall in May and June (Fig. 2B); while in July and August Tununuk Pt. shows intermediate values for precipitation. Tununuk Pt. has a wetter September than the other stations. Inuvik has a heavier snowfall than Tuktoyaktuk in May, August, and September. Cumulative normal winter snowfall values (Fig. 2C) probably underestimate snow accumulation in the taiga and overestimate it on the tundra due to the translocation of snow by wind (Hare 1971). Snow accumulation at Tununuk Pt. shows a similar pattern to that at Tuktoyaktuk. Much of the snowfall in May occurs early in the month, before snowmelt, and much of the snowfall in September occurs late in the month and usually stays.

METHODS

Live-trapping

Two 6.25 ha live-trap plots were set out approximately 4 km south-

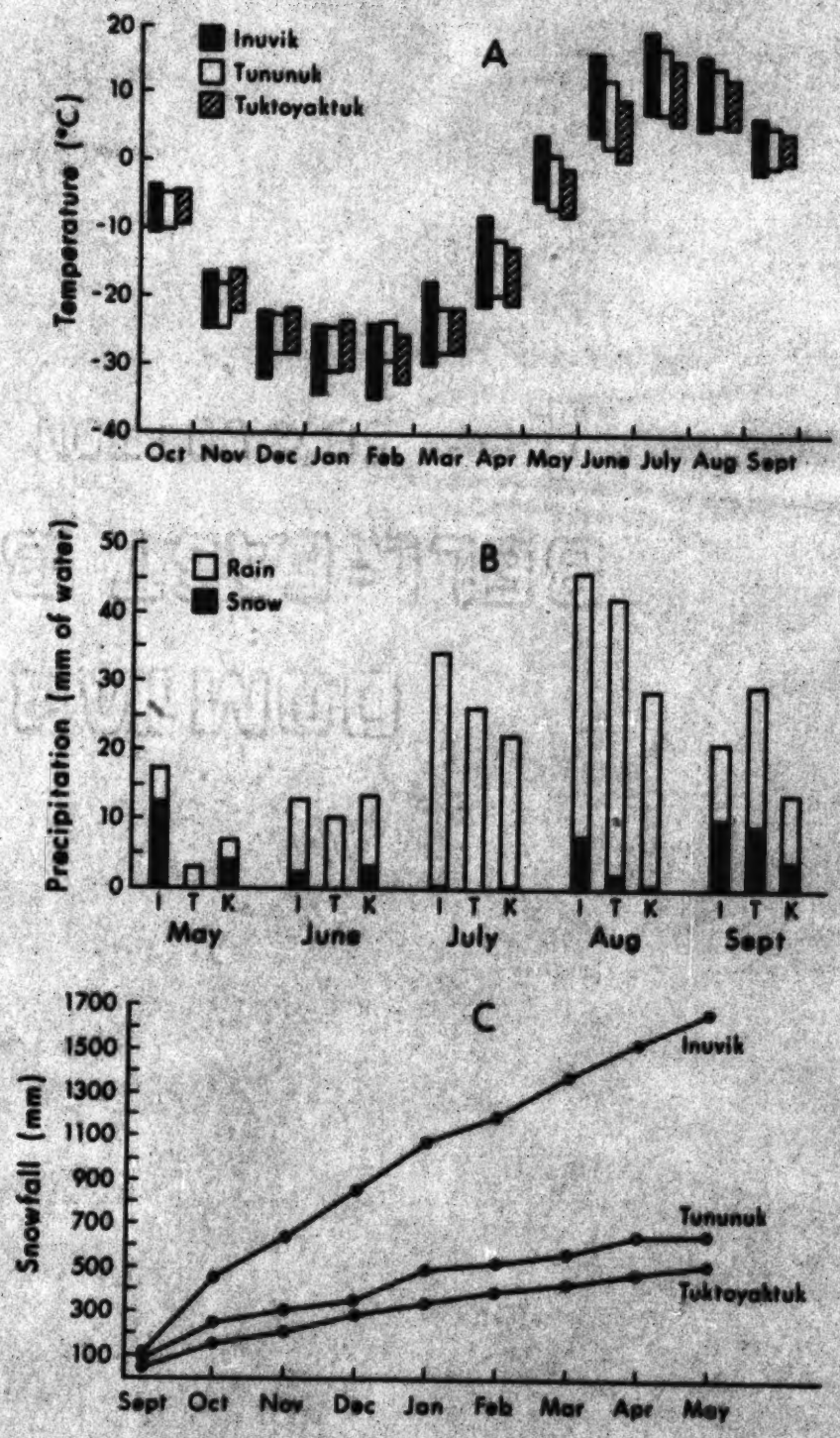

Figure 2. (A) Normal mean temperatures (maximum and minimum), (B) precipitation, and (C) cumulative snowfall for Inuvik (I), Tununuk Point (T), and Tuktoyaktuk (K).

east of Inuvik. Plot I lay across a small stream valley and was characterized by mature black spruce forest on the north-facing slope, white birch forest on the south-facing slope, and willow scrub in the bottom of the valley. Plot II lay entirely in black spruce forest. Without my prior knowledge, a winter road was cleared through Plot II on 20 April 1972 and a road was cleared across Plot I on the lower edge of the south-facing slope on 4 March 1973. I could do nothing about the 1972 road but I restored as much of the cleared slash as possible to the 1973 road before live-trapping began. A third 6.25 ha live-trap plot was set out approximately 3 km northeast of Tununuk Pt. in an area covered by a dwarf birch-heath and a sedge-cottongrass-heath community and the ecotone between the two. In all three plots, trap points were set out 25 m apart and two 7.6 x 7.6 x 22.9 cm (3 x 3 x 9 in.) folding Sherman live-traps were set at each point and covered with moss or litter. The traps were checked morning and evening, and all small mammals caught were toe-clipped, for later identification, on their first capture. Upon capture each small mammal was identified, sexed, weighed, and then released. Adults were separated from young-of-the-year on the basis of pelage and weight (adults > 21 g). In 1971 a total of 7,879 trap-nights were run on the Inuvik plots between June I* and August III, and 1,503 trap-nights were run on the Tununuk plot in June III and August II. In 1972 and 1973, 4,160 and 2,568 trap-nights respectively were run on the Inuvik plots between June II and July II.

Dead-trapping

Areas of well-developed black spruce forest, white birch forest

*Months were divided into three periods of approximately 10 days each: I, 1-10; II, 11-20; III, 21 - end of month. These divisions will be used regularly in the thesis.

and mixed forest within 6 km southeast of Inuvik were trapped periodically during the study. Trapping was done in a grid with trap lines normally 375 or 750 m long, trap points 15 m apart, and 15 m between lines. These distances are approximate since measurement was done by pacing. Two Victor "4-Way" snap traps were placed separately within a one-meter radius of each point and baited with a mixture of rolled oats, peanut butter, and almond extract. When snow cover was present, pits were dug in the snow and traps were set at ground level in alcoves off the main pit. Trap lines were normally run for 72 h and checked each 24 h. Each grid was approximately 2-9 ha in size and usually two (1-3) sites were trapped each trapping period. Any given site was trapped only once a year, usually at the same time of year. Altogether 52,997 trap-nights were run in the forest for population indices during the study: 7,047, May-October 1971; 3,300, November 1971 - April 1972; 21,438, May-October 1972; 21,192, April-September 1973. Approximately 22,000 supplementary trap-nights were run during the three years to obtain additional animals for autopsy.

Six shrub tundra areas, within a 15 km radius of Tununuk Pt., were dead-trapped. One additional area, approximately 11 km south of Tuktoyaktuk, was trapped in 1971. Trapping methods were the same as for forest areas except that trap lines were run in pairs rather than in grids. In 1971 the lines were usually 375 m long but in 1972 they were up to 2,250 m long and usually at least 1,125 m long; in 1973 they were normally 1,875 m long. A total of 44,104 trap-nights were run on the tundra for population indices during the study: 2,290, June-August 1971; 23,850, June-October 1972; 17,964, June-September 1973. Approximately 8,400 supplementary trap-nights were run during

the three summers to obtain additional animals for autopsy.

Autopsy

Measurements of total length, tail length, and hind foot length (to the nearest mm) and total weight (to the nearest 10 mg) were taken on all dead-trapped specimens. The skin was removed and checked for the presence of bites. The stomach was weighed to the nearest 10 mg and the adrenals, kidneys, and interscapular brown fat (BAT) body were preserved in AFA. After fixing at least one week, these organs were cleaned of external connective tissue, dried at room temperature, and weighed to the nearest 0.1 mg. Testis length was measured and epididymal smears were made to check for the presence of sperm when the testis length was 6-9 mm*. Female reproductive tracts were weighed to the nearest 10 mg and the number of embryos and/or placental scars, if present, was recorded. Tracts with embryos were preserved in AFA and embryos were examined later to estimate birth dates. Skulls were cleaned and condylobasal length was measured with calipers to the nearest 0.05 mm.

Age Determination

Age of embryos was determined by two techniques. Embryos were removed from their membranes and examined under a dissecting microscope (usually at 10-20x) for the stage of development (Tupikova 1964) and weighed (to the nearest 0.01 g) to determine conception age (Huggett and Widdas 1951). Normally four embryos were weighed together and the

*Examination of epididymal smears of all males in the summer of 1971 showed that males with a testis length of 10 mm or greater and macroscopic epididymal tubules always had sperm in the epididymis (functional); those with a testis length of 5 mm or less and microscopic tubules never had sperm in the epididymis (non-functional).

mean was recorded. It was very difficult to dissect out and weigh embryos weighing less than 0.02 g; therefore, a number of such litters were not weighed. Using Tupikova's tables the age of the embryos was determined by the external appearance of the uterus and embryos for the period of 11-12 days before birth and by the developmental characteristics of the embryo for the period from 10 days before birth to birth. I did not feel that pregnancies could be determined with any confidence earlier than 12 days before birth.

Huggett and Widdas' technique requires an estimation of gestation period and weight at birth. Gestation period was taken to be 17 days since Koshkina (1957) reported 16-17 days for *C. rutilus*; Svihla (1930) found 17-19 days, usually 17, for *C. gapperi*; Wrangel (1940) gave 17.5-18 days for *C. glareolus*; and two litters of *C. rutilus* born in captivity during the study had maximum gestation periods of 17 days. Morrison *et al.* (1954) found the average birth weight of *C. rutilus*, based on six litters, to be 1.71 g (1.55-1.95). Koshkina (1957) gave a range of 1.4-1.75 g, but the two largest embryos found in the present study were 1.84 and 1.86 g. Birth weight was considered to be 1.71 g.

Age of dead-trapped animals was estimated from the development of the second upper molar (M2) (Tupikova *et al.* 1968, Viitala 1971). Cleaned skulls were examined under a dissecting microscope at 20x and M2 (normally right) was exposed by flaking away the bone covering it. The stage of development of the tooth was noted and the root length, from the closure of the anterior groove along the anterior root, was measured to the nearest 0.1 mm using an ocular grid.

Four successive stages in development of the tooth were noted (Fig. 3): (i) anterior groove open, (ii) anterior groove closed,

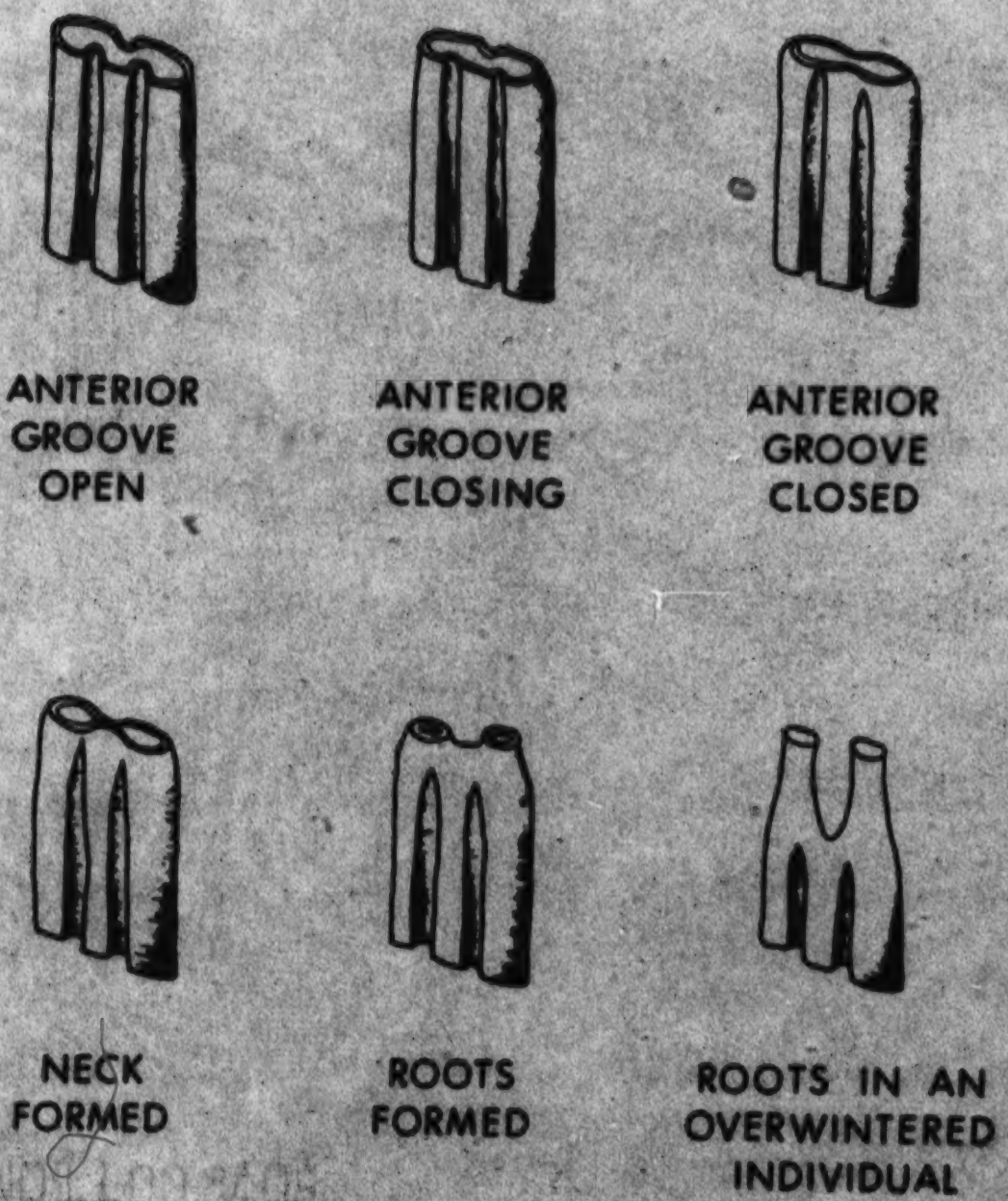

Figure 3. Sketches of the labial aspect of the second upper molar (M2) of *C. rutilus* showing the characteristics used in age determination. Anterior is to the right.

(iii) neck formed, (iv) roots formed. Overwintered animals were easily distinguishable by the presence of long roots (> 1.0 mm, mid-June through October). Non-overwintered animals were separated into two groups depending on the degree of M2 development; the group with more advanced M2 development was divided into reproductively active (functional testes in males and embryos or placental scars in females) and non-reproductively active individuals.

Weather

Data on temperature, precipitation, and snow accumulation were compiled from Environment Canada, Atmospheric Environment Service records for Inuvik and Tuktoyaktuk for the period September 1970 to September 1973. Conversions were made from English to metric units.

During the winter of 1971-72 and 1972-73 snow surveys were carried out at three locations near taiga live-trap plot I and at two locations near the tundra live-trap plot. At each site snow depth was measured at 12 points and thickness and density of each layer of the snow cover was measured at one point using instruments and methods devised by the National Research Council of Canada (Klein *et al.* 1950). Depth of snow at the density-measuring point and thickness of each layer in the snow cover were adjusted to the mean snow depth for the site.

Thermal resistance is directly proportional to thickness of insulation and inversely proportional to thermal conductivity, and thermal conductivity of snow is directly proportional to the square of the density. Therefore, an index of thermal resistance of snow cover was calculated by the following equation: $I_{TR} = \sum_{i=1}^{n} (t_i/d_i^2)$

where t_i and d_i are the thickness and density, respectively, of layer i of the snow cover.

Statistics

Statistical procedures used follow Sokal and Rohlf (1969). When significant differences were found in variances the appropriate adjusted t-test or F-test was run. Because of this the actual test values are not presented, although the test used and the probability level is. For the purposes of uniformity Chi-square (X^2) test results will be presented in the same manner.

RESULTS

Taiga Population

Population levels

The population level at snowmelt declined each year from 1971 to 1973; while the peak summer level was highest in 1971, lowest in 1972, and high again in 1973 (Fig. 4, Appendix 1). Between 1 June and 15 September the population increased 75% in 1971 and 80% in 1972 but increased 466% in 1973. The population showed a winter (September III - June I) decrease of 76% in 1971-72 and 55% in 1972-73. Between August III 1971 and June II 1972 there was a decline of 85% in the total number of *C. rutilus* on live-trap Plot I and 99% in marked animals. The estimated decrease for the same period from dead-trap data was 78%. There was a marked decline in population (27%) in September 1972 but not in September 1971.

Age structure

Comparison of the days to birth of each litter as determined by

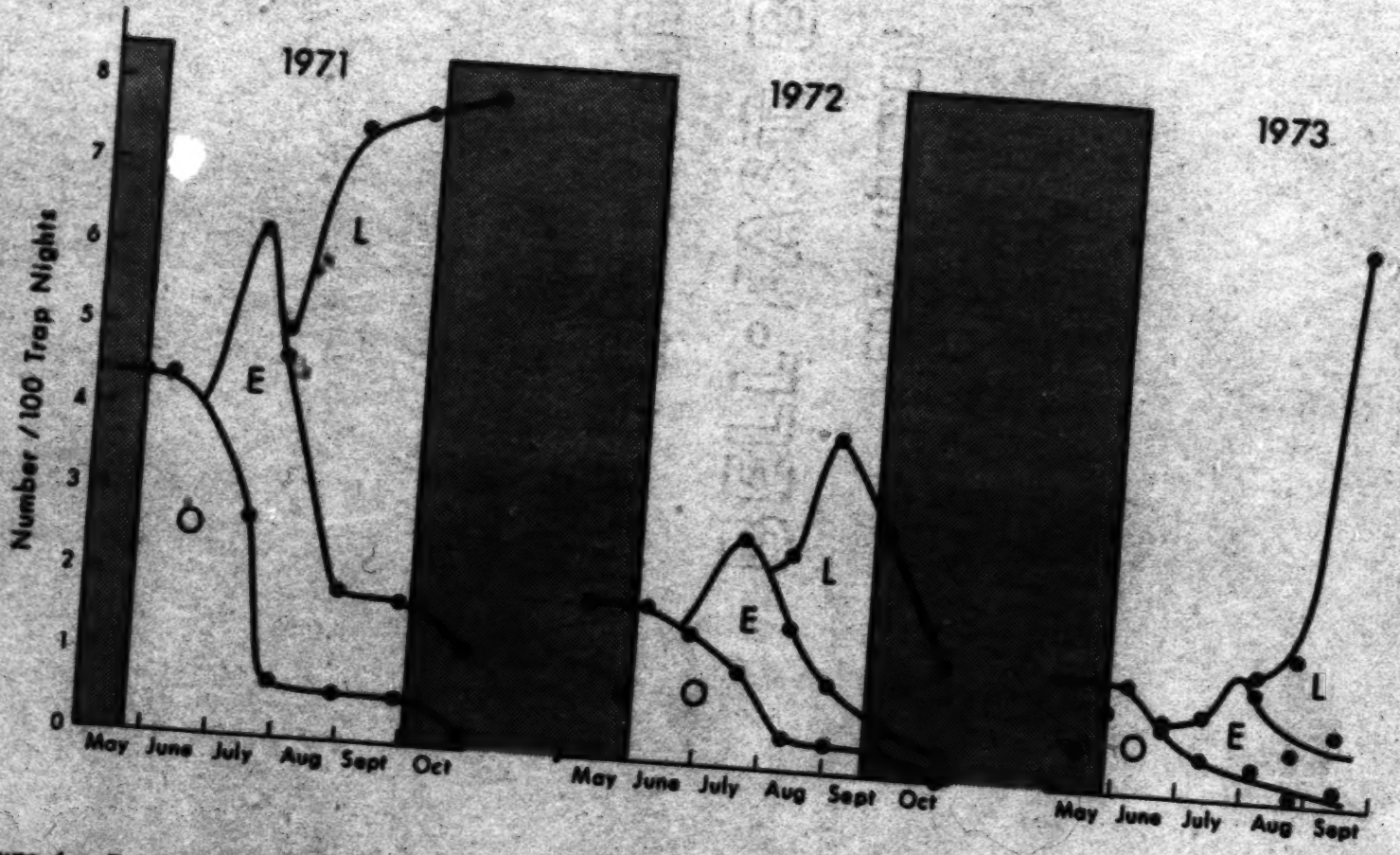

Figure 4. Taiga population indices showing the overwintered (O), early-cohort (E), and late-cohort (L) components. The periods of snowcover are shaded.

Huggett and Widdas' and Tupikova's techniques (Table 2)* showed that the average difference between the two independent estimates was 0.61 ± 0.054 days. The greatest observed difference was 1.8 days.

When birth dates were plotted (Fig. 5), it was apparent that young are produced in two relatively easily separable groups: those born in June and those born in July and August. The first group - 'early cohort' - consists of the first litter of overwintered females and the second group - 'late cohort' - consists of the second litter of overwintered females and the first and second litters of young-of-the-year.

During the study, eight litters were raised in captivity and, in all cases, young first emerged from the nest at 15 or 16 days of age. Measurements of young from three of these litters (Table 3) suggest that animals less than 25 days old are easily separable from older individuals. Morrison *et al.* (1954) have shown linear growth for the first 20 days of life for *C. rutilus*.

Based on the assumption that juveniles cannot be trapped before 15 days of age and the information on birth dates, the age of members of each cohort in each trapping period was determined (Table 5). Comparison of cohort ages and distribution of M2 characteristics in young-of-the-year in summer trapping periods (Table 4) indicate ages for formation of M2 characteristics (Table 6). Different rates of development are indicated for the two cohorts and for reproductively active and non-reproductively active members of the early cohort. Ages for development of M2 characteristics of non-reproductive members of the early cohort are essentially the same as those presented by Tupikova *et al.* (1968) for *C. rutilus* and *C. glareolus* and show the same trend as those ages

*Data from tundra animals were included in this analysis

Table 2. Comparison of the Huggett and Widdas (1951) and Tupikova (1964) techniques of determining the age of embryos.

Sample size	Embryo weight	Huggett and Widdas Days to birth	Tupikova Mean Days to birth	Tupikova Range
4	0.005	8.7	10.0	(9-10,10-11)
5	0.01	8.3	8.6	(7-8, 10)
15	0.02	7.9	8.5	(7-8, 9)
3	0.03	7.5	8	
7	0.04	7.3	7.4	(7, 8)
4	0.05	7.0	7.1	(7, 7-8)
7	0.06	6.9	6.9	(6-7, 7)
3	0.07	6.7	7.3	(7, 8)
3	0.08	6.6	6.8	(6-7, 7)
2	0.09	6.4	6.2	(6, 6-7)
1	0.10	6.2	7	
2	0.11	6.1	5.5	(5, 6)
1	0.12	6.0	6	
3	0.14	5.7	6.2	(6, 6-7)
2	0.16	5.6	6	
1	0.17	5.5	6	
1	0.18	5.4	6	
2	0.20	5.2	5	(4-5,5-6)
1	0.24	4.9	6	
1	0.26	4.8	5-6	
1	0.28	4.6	5-6	
2	0.29	4.5	5.2	(5, 5-6)
2	0.30	4.5	4.5	(4, 5)
2	0.33	4.3	5.2	(5, 5-6)
1	0.34	4.2	5-6	
1	0.37	4.1	5-6	
1	0.38	4.0	5-6	
1	0.40	4.0	5-6	
1	0.42	3.8	5	
2	0.43	3.8	5.5	(2-3, 4-5)
1	0.44	3.7	5-6	
1	0.47	3.6	5	
2	0.50	3.4	4.8	(4-5, 5)
1	0.52	3.3	4	
1	0.53	3.3	4-5	
1	0.58	3.1	4-5	
2	0.64	2.8	1.8	(1, 2-3)
1	0.66	2.8	2-3	
1	0.71	2.6	2-3	
2	0.81	2.2	1.8	(1, 2-3)
1	0.84	2.1	1	
3	1.00	1.7	1-2	
1	1.04	1.6	2-3	
1	1.07	1.4	2-3	
1	1.08	1.4	1-2	
1	1.11	1.4	1	
2	1.14	1.3	1	
1	1.16	1.2	1-2	
1	1.20	1.1	1	
1	1.21	1.1	1	
1	1.22	1.1	1	
1	1.25	1.0	1-2	
1	1.30	0.9	1	
1	1.35	0.8	1	
1	1.36	0.7	1	
1	1.37	0.7	1	
1	1.45	0.5	1	
1	1.52	0.4	1	
1	1.54	0.3	1	
1	1.60	0.2	1	
1	1.68	0.0	1	
1	1.69	0.0	1	
1	1.84	-0.3	1	
1	1.86	-0.3	1	

Table 3. Measurements of animals raised in captivity (mean and range).

Age (days)	Sample size	Body weight (gms)	Body length (mm)	Condylobasal length (mm)	Zygomatic breadth (mm)	M2 tooth length (mm)
15	2	7.865 (7.72- 8.01)	70.0 (70)	18.35*		2.00 (2.0)
20	4	10.145 (9.53-11.13)	75.8 (74-77)	19.638 (19.25-20.25)	11.400** (11.30-11.50)	2.60 (2.5-2.7)
25	4	13.640 (12.34-14.88)	90.0 (86-95)	21.350 (20.40-21.75)	11.775 (11.40-12.10)	3.02 (2.9-3.1)
30	5	17.526 (14.42-20.26)	89.8 (86-93)	21.840 (21.40-22.15)	12.090 (11.85-12.35)	3.04 (3.0-3.1)

* sample size of 1
** sample size of 3

Table 4. Distribution of M2 characteristics in taiga animals, adjusted sample sizes.

trapping period	Early Cohort (Reproductively Active males and females) Sample size	Groove open %	Groove closed %	Neck formed %	Roots formed %	Early Cohort (Non-reproductively Active males and females) Sample size	Groove open %	Groove closed %	Neck formed %	Roots formed %	Late Cohort (males and females) Sample size	Groove open %	Groove closed %	Neck formed %	Roots formed %
1971															
July 14	14	100													
July 28	3	67	33			45	100								
Aug 28	6		17	33	50	11	82	18			2	100			
Sept 25	4			25	75	26		46	54		152	100			
Oct 28	4				100	19			100		118	35	65		
1972						2				100	45			80	20
June 25															
July 18						1	100								
Aug 10	6	33	17	33	17	49	100								
Sept 1	9		22	33	44	36	53	47							
Sept 24	5			80	20	12		92	8		52	100			
Oct 24	2				100	10			80	20	80	100			
1973						8				100	82	42	58		
June 21											35	3	34	63	
July 11	2	100				2	100								
Aug 4	20	15	35	40	10	12	100								
Aug 22	12			50	50	10	60	40			7	100			
Sept 13	15			27	73	4		25	75		54	100			
						7			100		302	86	14		

Table 5. Calculated ages of taiga young-of-the-year in the sampling periods.

Mid-point of trapping period	Age (days) Early cohort	Late cohort
1971		
July 14	27 - 40	
July 28	41 - 54	
Aug. 28	72 - 85	15 - 43
Sept. 25	100 - 113	19 - 71
Oct. 28	133 - 146	52 - 104
1972		
June 25	15 - 19	
July 18	15 - 42	
Aug. 10	33 - 65	15 - 31
Sept. 1	55 - 87	15 - 53
Sept. 24	78 - 110	18 - 76
Oct. 24	108 - 140	47 - 106
1973		
June 21	15 - 20	
July 11	15 - 40	
Aug. 4	39 - 64	15 - 33
Aug. 22	57 - 82	15 - 51
Sept. 13	79 - 104	15 - 73

Table 6. Approximate ages, in days, between which formation of indicated M2 characteristics occurs in taiga animals.

	Groove closed	Neck formed	Roots formed
Early cohort - reproductive	40 - 50	± 55	55 - 65
Early cohort - non-reproductive	45 - 55	65 - 75	± 110
Late Cohort	55 - 70	75 - 105	105 - 120

presented by Viitala (1971) for *C. rufocanus*, a slower growing species. A slower rate of development has been suggested (Tupikova *et al.* 1968) and demonstrated (Viitala 1971, Lowe 1971) for late cohorts in *Clethrionomys*.

The separation of cohorts is clear during most sampling periods; however, in two periods (10 August 1972, 4 August 1973) early cohort non-reproductive tended to be overestimated and late cohort underestimated because the 25-55 day old animals were not separated by the M2 characteristics measured. M2 in these two samples was then re-examined to subjectively separate the cohorts based on degree of closure of the anterior groove. Animals with the anterior groove closing were retained in the early cohort; those with the anterior groove broadly open were shifted to the late cohort. Re-examination resulted in a reassignment of 24 animals from early cohort non-reproductive to late cohort in the 1972 sample and six in 1973. The adjusted distribution was used in further analysis. The representation of each age class in the population May-October 1971-73 is presented in Figure 4 and Appendix 1.

Sex ratio

Sex ratios of all dead-trapped animals caught during index trapping were examined (Table 7) and only a few significant differences from a 1:1 ratio were found. Although highly significant differences were found July II 1971 and June I 1972, live-trap samples taken at approximately the same time failed to show any significant deviation from a 1:1 ratio (Table 25). There were no significant differences between years in mean sex ratio of each age class.

There was a general pattern in overwintered animals for an excess

Table 7. Sex ratios (proportion of males) based on taiga index trapping catches (sample size in parentheses) and compared to a 1:1 ratio by goodness of fit X^2.

Sampling period		1971		1972		1973	
				Overwintered			
Apr	I					.500	(12)
	II			.500	(4)		
May	I			.500	(8)	.667	(3)
	III	.727	(11)	.444	(9)	.643	(28)
June	I	.615	(39)	.692**	(65)	.583	(36)
	III			.586	(29)	.545	(22)
July	II	.778**	(27)	.514	(35)	.750	(12)
	III	.500	(2)				
Aug	I			.461	(13)	.428	(14)
	III	.417	(12)	.333	(9)	.333	(3)
Sept	II					.000	(5)
	III	.100*	(10)	.333	(9)		
Oct	III	.000	(1)				
Total		.588	(102)	.563	(181)	.556	(135)
				Early cohort			
June	III					1.000	(2)
July	II	.417	(36)	.592	(49)	.417	(12)
	III	.417	(12)				
Aug	I			.561	(41)	.367	(30)
	III	.643	(28)	.450	(20)	.500	(16)
Sept	II					.375	(16)
	III	.571	(21)	.500	(10)		
Oct	III	.167	(6)	.300	(10)		
Total		.495	(103)	.531	(130)	.421	(76)
				Late cohort			
July	III	1.000	(1)				
Aug	I			.724*	(29)	.857	(7)
	III	.540	(124)	.494	(79)	.515	(33)
Sept	II					.598*	(142)
	III	.551	(107)	.580	(69)		
Oct	III	.425	(40)	.500	(32)		
Total		.529	(272)	.555	(209)	.598*	(182)

* $0.05 > p > 0.01$
** $0.01 > p > 0.001$

of males in early summer and for a deficiency in late summer. May III - June I sex ratios were significantly different from August III - September III sex ratios in each year (X^2 test: 1971 and 1973, $0.001 > p > 0.01$; 1972, $0.05 > p > 0.01$). This shift in sex ratio may have been due to decreased trappability of females when pregnant and nursing, increased summer mortality among males related to their greater mobility (males have larger home ranges than females), or a combination of the two. The combination of factors is the most likely explanation since late-cohort animals October III 1971 and 1972 and overwintered animals April II and May I 1972 and April I 1973 showed no excess of males indicating that the overwintering populations had very close to a 1:1 ratio.

Reproduction

In all three years the first conception took place during the third week of May and the breeding seasons (first to last conception) were 89, 94, and 119 days for 1971, 1972, and 1973 respectively. The apparently longer breeding season in 1973 was because one female was found pregnant in mid-September; if this animal were excluded the season would have been 93 days. Examination of birth dates of litters (Fig. 5) indicates that in 1972 the mean birth date of the first litter of overwintered females was delayed about 11 days, and the second litter about 5 days, relative to the other two years.

In all three years, 100% of overwintered females produced a first litter and an average of 84% of survivors to July II - October III produced a second litter (Table 8) with no significant differences between years. An average of 45% of early-cohort females produced a first litter in 1971 and 1972 but 77%, significantly more, did in 1973 (Table 9). An

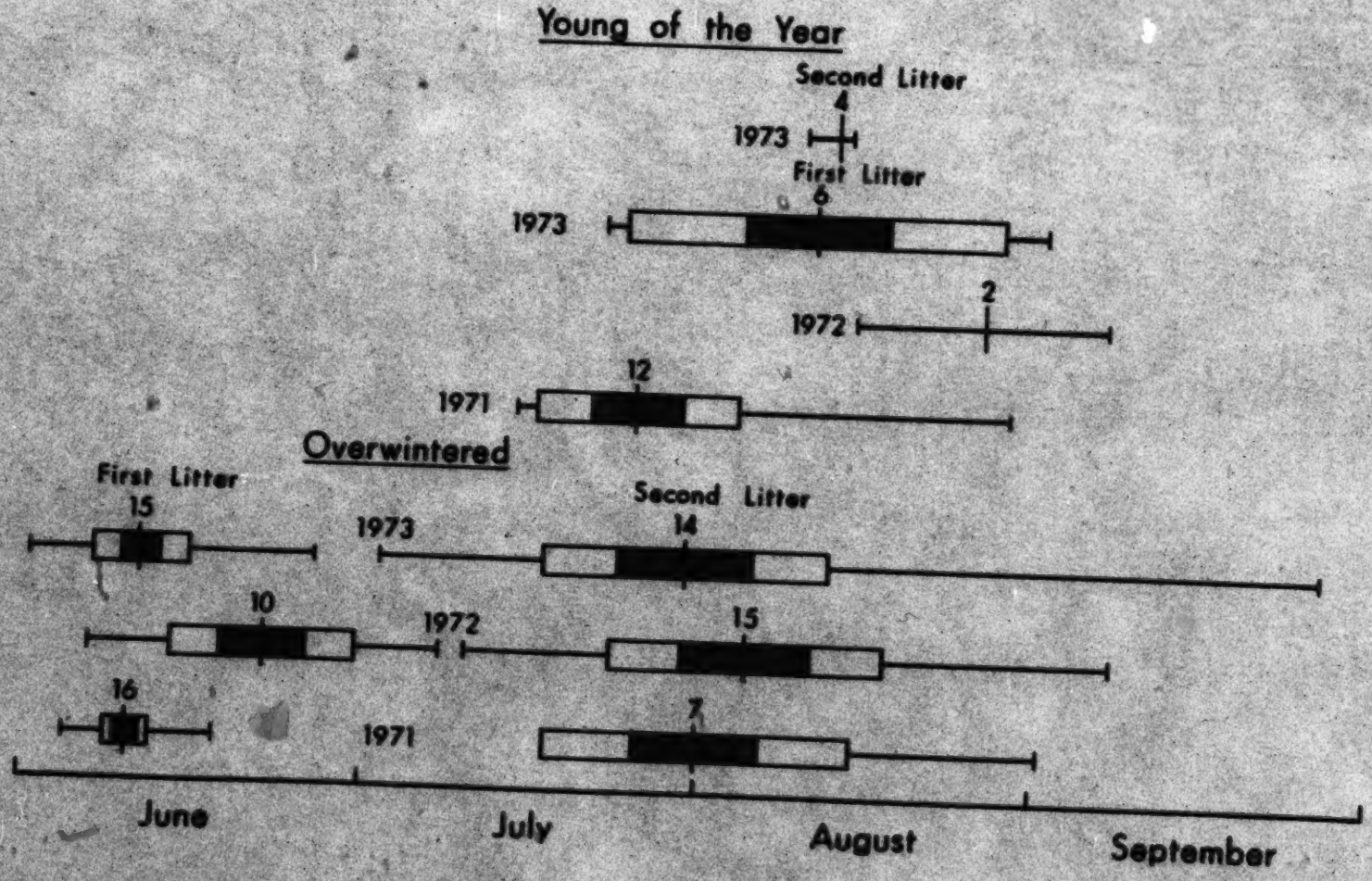

Figure 5. Birth dates for taiga litters based on embryo ages. Mean ± SE ± 95% CL, range, and sample size are presented in each case, except where the sample is less than 5.

Table 8. Proportion of taiga breeding females captured July II-October III* that produced a second litter, based on placental scar counts. Significance of differences between years by X^2 test is indicated.

Year	Overwintered %	Overwintered sample size	Early cohort %	Early cohort sample size
1971	85.7	(28)	7.1	(14)
1972	85.2	(27)	6.7	(15)
1973	81.0	(21)	22.8	(35)
(71,72,73)	$0.9 > p > 0.5$		$0.5 > p > 0.1$	

* The July II 1972 sample was not considered due to the delayed breeding season.

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Table 9. Proportion of taiga early-cohort females with embryos and/or placental scars. Significance of difference between July II-October III means by X^2 test is indicated.

Sampling period		1971 %	1971 sample size	1972 %	1972 sample size	1973 %	1973 sample size
July	I	0.0	(4)				
	II	46.2	(26)	0.0	(20)	28.6	(7)
	III	28.6	(7)				
Aug	I			33.3	(18)	84.2	(19)
	II						
	III	46.2	(13)	72.7	(11)	87.5	(8)
Sept	I						
	II					85.7	(14)
	III	36.4	(11)	50.0	(10)		
Oct	I						
	II						
	III	80.0	(5)	28.6	(7)		
Mean		45.2	(62)	45.6	(46)	77.1	(48)

(71-72) $p > 0.9$
(71-73) $p < 0.001$
(72-73) $p < 0.01$

* The July II 1972 sample was not considered due to the delayed breeding season.

average of 16% of early-cohort breeders surviving to July II - October III had a second litter (Table 8) with no significant differences between years. Pregnancy in late-cohort females was rare: 0.9% (1) of the females in 1973. There was no indisputable evidence of a third litter being produced by any female. Although some variation occurred in litter sizes (Table 10), there was no significant difference in litter size between litters, years, or age class of females (F test, $0.10 > p > 0.05$).

Overwintered males became functional during late April in 1972 and 1973 (Fig. 6) and remained that way through the end of September in 1972 but ceased earlier in the other two years. Regressing males were first found August III in all three years. June-August testis length for overwintered males was significantly less in 1973 than in the other two years (Fig. 6); no differences were observed in non-breeding males. All males examined October 1971 - March 1972 had a testis length of 3 mm. An average of 2.8% of early-cohort males became functional in 1971 and 1972 but 37.5%, significantly more, did in 1973 (Table 11).

Wounding

The frequency of wounding in animals tended to be highest during July and August (Appendix 2). The mean frequencies of males and females wounded (Tables 12 and 13) were compared by age class in each year. Significantly more overwintered males than overwintered females had wounds in 1971 and 1973 (χ^2 test, $p < 0.001$ and $0.05 > p > 0.01$ respectively) and significantly more late-cohort males than late-cohort females were wounded in 1971 (χ^2 test, $p < 0.001$), but these were the only significant differences between sexes. Comparisons were also made

Table 10. Taiga litter sizes, based on embryo count, and degree of resorption.

	First Litter				Second Litter			
		Total count		Resorbing		Total count		Resorbing
Year	Sample size	Mean ± SE and Range	% Females	Mean no. of embryos	Sample size	Mean ± SE and Range	% Females	Mean no. of embryos
Overwintered								
1971	(16)	7.00 ± 0.182 (6-8)	12	0.12	(7)	7.71 ± 0.474 (6-10)	28	0.43
1972	(11)	6.45 ± 0.493 (4-9)	0		(15)	6.80 ± 0.200 (5-8)	7	0.07
1973	(15)	6.40 ± 0.235 (5-8)	7	0.07	(14)	7.21 ± 0.380 (4-9)	7	0.43
Early cohort								
1971	(12)	6.17 ± 0.322 (4-8)	17	0.33	(0)			
1972	(4)	6.00 ± 0.408 (5-7)	25	1.50	(0)			
1973	(6)	6.17 ± 0.543 (4-8)	0		(4)	6.00 ± 0.408 (5-7)	0	

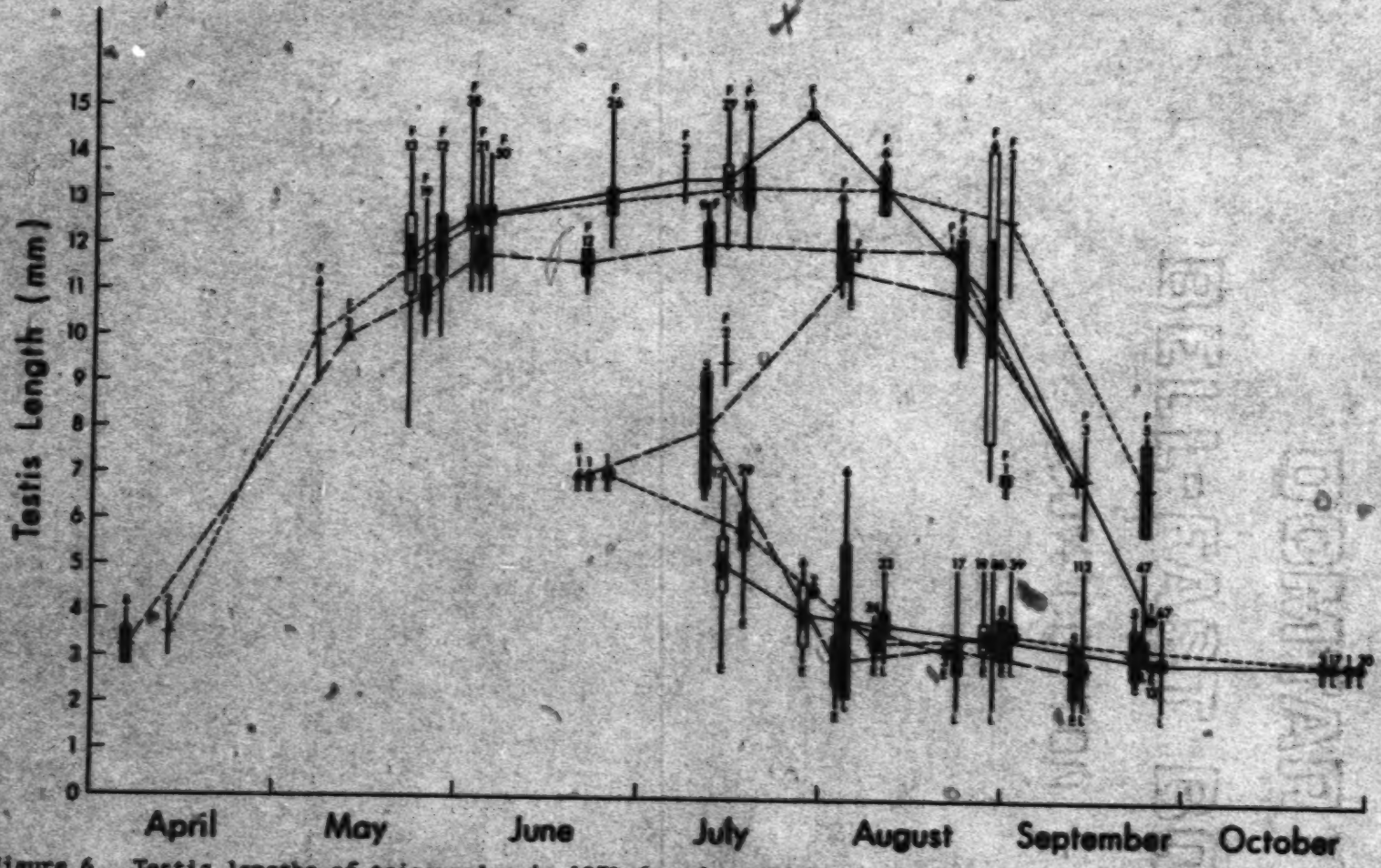

Figure 6. Testis lengths of taiga males in 1971 (open), 1972 (heavy bars), and 1973 (light bars). Early- and late-cohort males are designated by an "E" or "L" respectively below the bar; overwintered males have no mark below the bar. Punctional males are indicated by an "P" above the bar. Mean ± SE ± 95% CL, range, and sample size are presented for samples of 5 or more; mean, range, and sample size are presented for samples of less than 5.

Table 11. Proportion of taiga early-cohort males functional. Significance of differences between July II-August III means by X^2 test are indicated.

Sampling period	1971 %	1971 Sample size	1972 %	1972 Sample size	1973 %	1973 Sample size
June III			0.0	(1)	50.0	(2)
July I						
II	10.5	(19)	0.0	(29)	0.0	(5)
III	0.0	(6)				
Aug I			0.0	(24)	36.4	(11)
II						
III	0.0	(19)	11.1	(9)	62.5	(8)
Sept I						
II					37.5	(8)
III	0.0	(12)	0.0	(5)		
Oct I						
II						
III	0.0	(1)	0.0	(3)		
Mean	4.5	(44)	1.6	(62)	37.5	(24)

(71-72) $0.5 > p > 0.1$
(71-73) $p < 0.001$
(72-73) $p < 0.001$

Table 12. Mean June-September proportion of taiga animals with wounds. Significance of differences between years by X^2 test are indicated.

Year	Overwintered %	Overwintered sample size	Early cohort %	Early cohort sample size	Late cohort %	Late cohort sample size
Males						
1971	73.7	(38)	19.6	(56)	12.2	(155)
1972	9.0	(111)	4.4	(68)	0.9	(109)
1973	14.0	(50)	14.7	(34)	2.2	(135)
(71-72)	***		**		***	
(71-73)	***		n.s.		**	
(72-73)	n.s.		n.s.		n.s.	
Females						
1971	21.4	(28)	23.0	(61)	0.8	(117)
1972	2.4	(84)	6.8	(59)	0.0	(85)
1973	2.2	(46)	8.3	(48)	0.0	(107)
(71-72)	***		*		n.s.	
(71-73)	**		*		n.s.	
(72-73)	n.s.		n.s.		n.s.	

n.s. (not significant) $p > 0.05$
* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $p < 0.001$

Table 13. Mean June-September proportion of early-cohort taiga animals with wounds. Significance of differences related to breeding status and years by X^2 test are indicated.

Year	breeding %	breeding sample size	non-breeding %	non-breeding sample size	(breeding - non-breeding)
Males					
1971	100.0	(2)	16.7	(54)	**
1972	0.0	(1)	4.5	(67)	n.s.
1973	23.1	(13)	9.5	(21)	n.s.
(71-72)	n.s.		*		
(71-73)	*		n.s.		
(72-73)	n.s.		n.s.		
Females					
1971	37.5	(24)	13.5	(37)	*
1972	15.8	(19)	2.5	(40)	n.s.
1973	8.1	(37)	9.1	(11)	n.s.
(71-72)	n.s.		n.s.		
(71-73)	**		n.s.		
(72-73)	n.s.		n.s.		

n.s. (not significant) = $p > 0.05$
* $0.05 > p > 0.01$
** $0.01 > p > 0.001$

within each age-sex class between years (Table 12) and, in general, there was significantly more wounding in 1971 than in the other two years. When early-cohort animals were considered in relation to breeding status (Table 13) the trend was still present but not as definite. Also, 1971 was the only year in which significantly more early-cohort breeders than non-breeders were wounded.

Organ weights

Fresh, fixed, and dry adrenal, kidney, and BAT weights of 11 animals trapped April I 1973, and fresh and dry kidney weights of 44 animals trapped August III 1971 were compared. There were no significant differences between mean fresh and fixed weight of any organ (t-test, $0.9 > p > 0.5$, for all organs). Dry weights of organs were significantly correlated with their fresh weights (correlation coefficients: adrenal = 0.64, $0.05 > p > 0.01$; kidney = 0.96, $p < 0.001$; BAT = 0.91, $p < 0.001$). Mean dry weight as a percentage of mean fresh weight was 50.9% for adrenals, 27.9% for kidneys, and 54.8% for BAT.

Data on organ weights were analysed separately and only differences between years and summarized data are presented. Organ weights of animals judged to be less than 25 days old (Table 3) were eliminated from analysis since this is the period of most rapid growth.

(i) adrenal

In overwintered animals the only marked differences between years occurred May III 1971 when both males and females had significantly heavier adrenals than in the other two years (F test, $p < 0.001$) (Appendix 3); by June I this difference was no longer significant. There were no marked differences

in adrenal weight between years in early-cohort animals but adrenals of late-cohort animals tended to be heaviest in 1973 and lightest in 1971. There were no significant changes in adrenal weight during the winter of 1971-72 (Appendix 6).

(ii) kidney

Kidney weights were relatively similar between years in early summer and late summer. However, early summer weights tended to be highest in 1971 and lowest in 1973 while late summer weights tended to be higher in 1972 than in the other two years. The most marked difference between years occurred in mid-summer when values were highest in 1972 and lowest in 1971. There was a marked drop in kidney weight September III to October III in 1971 but not in 1972. Essentially no change in kidney weight occurred October III 1971 to April II 1972 (Appendix 6) but weights were notably higher in October III 1972 and April I 1973 than in the preceding winter.

(iii) BAT

Interscapular BAT weights tended to be highest in early and late summer 1971 and lowest in late summer 1973 (Appendix 5). There were no marked differences in BAT weights between 1971 and 1972 in September III or October III or between 1972 and 1973 in April and May.

Growth

Growth was measured by three parameters: body length (total length minus tail length), condylobasal length, and corrected body weight (total body weight minus stomach weight and, in females, reproductive

tract weight). Animals judged to be less than 25 days old (Table 3) were eliminated from analysis since this is the period of most rapid growth. Mean body measurements (Appendices 7, 8, and 9) and the significance of differences between males and females (Appendix 10) are presented.

Growth in overwintered animals in 1971 was significantly less than in the other two years in body length and markedly (but not significantly) less in condylobasal length (Figs. 7 and 8). Growth in body length in young-of-the-year was also significantly less in 1971. There were no marked differences between years in body weight (Fig. 9).

No significant changes in the growth parameters were observed November 1971 - April 1972 (Fig. 10). A significant drop in corrected body weight was observed in 1971 and 1972 during October (Fig. 9). New growth in body length did not begin until late May but growth in the other two parameters appeared to begin as early as April (Figs. 7-10).

Disappearance rates

The summer disappearance rate of overwintered animals was calculated by comparing early summer (May III - June I) and late summer (Aug. III - Sept. III) dead-trap indices (Fig. 4, Appendix 1). An average of 86% of the overwintered animals disappeared over 3-4 months during the summer (1971, 87.2%; 1972, 83.0%; 1973, 86.2%) with no significant differences between years (X^2 test, $p > 0.9$).

A measure of disappearance in early and late cohorts was established by calculating the maximum number of young which could have been produced and comparing this value with the number observed at the date when it would be expected from reproductive data that no new individuals could be

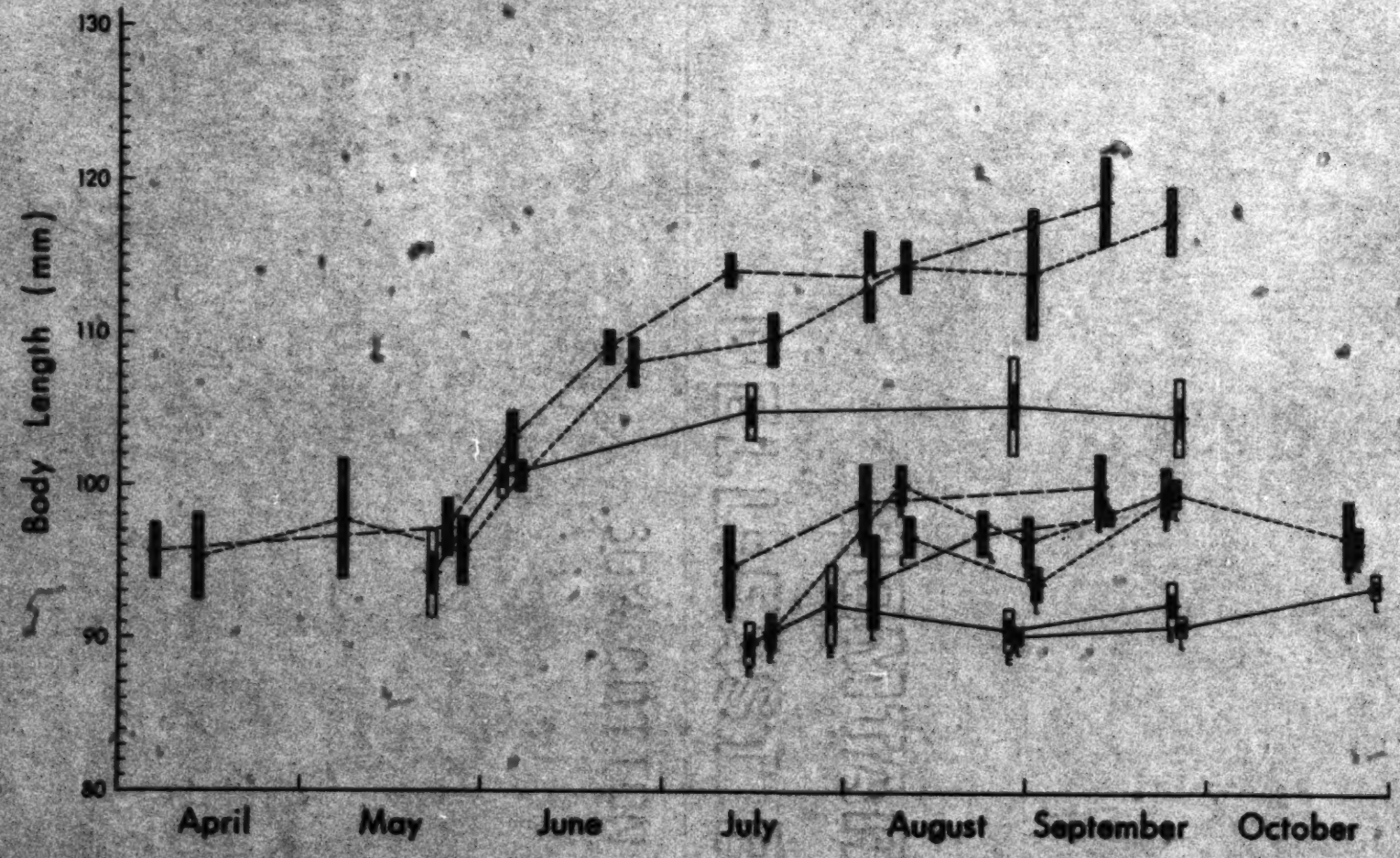

Figure 7. Body length of overwintered, early-cohort non-breeding (E) and late-cohort (L) taiga animals (sexes combined) in 1971 (open), 1972 (heavy bars), and 1973 (light bars). Mean ± SE ± 95% CL are shown for sample sizes of 5 or greater.

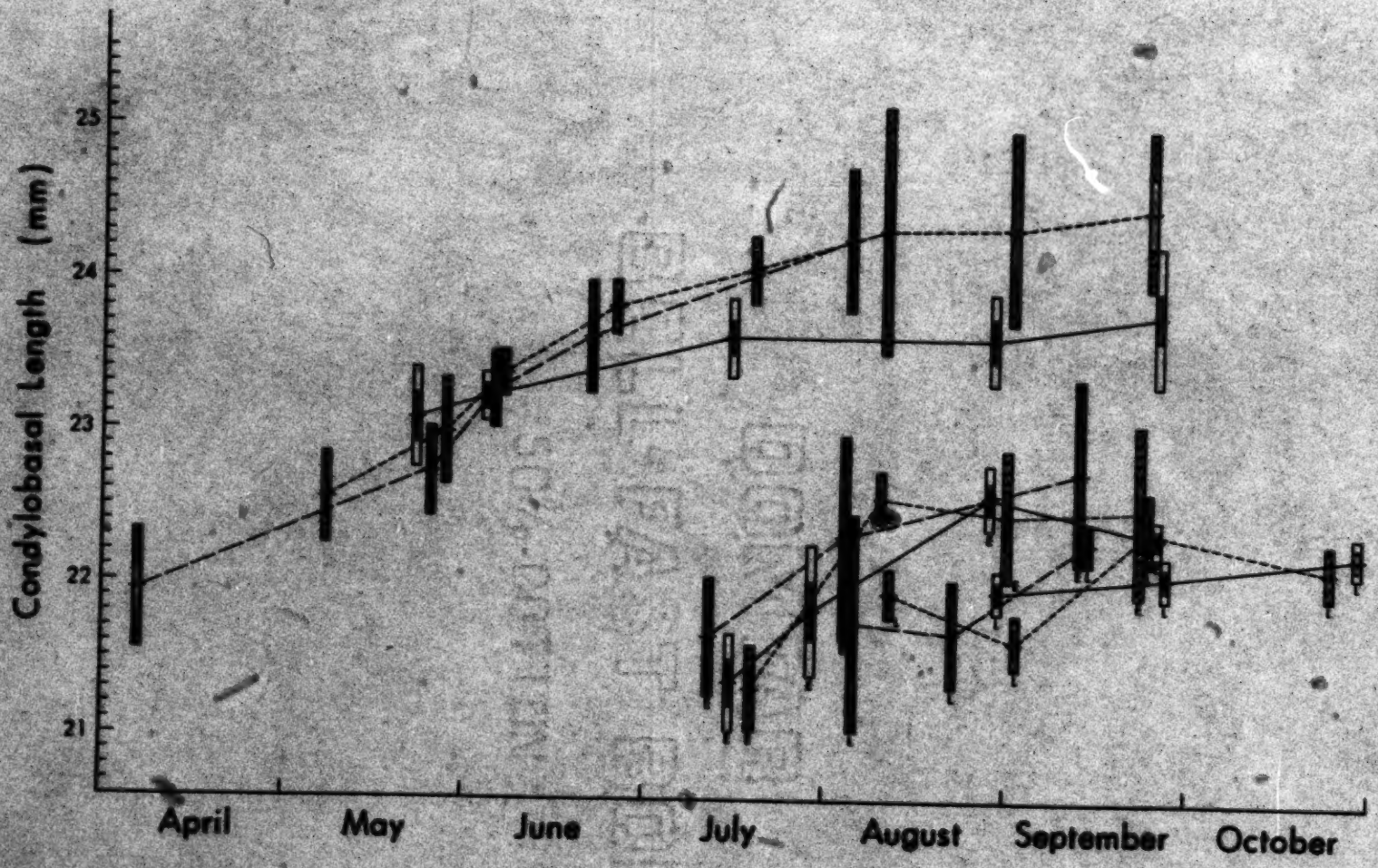

Figure 8. Condylobasal length of taiga animals 1971-1973. Symbols are the same as in Fig. 7.

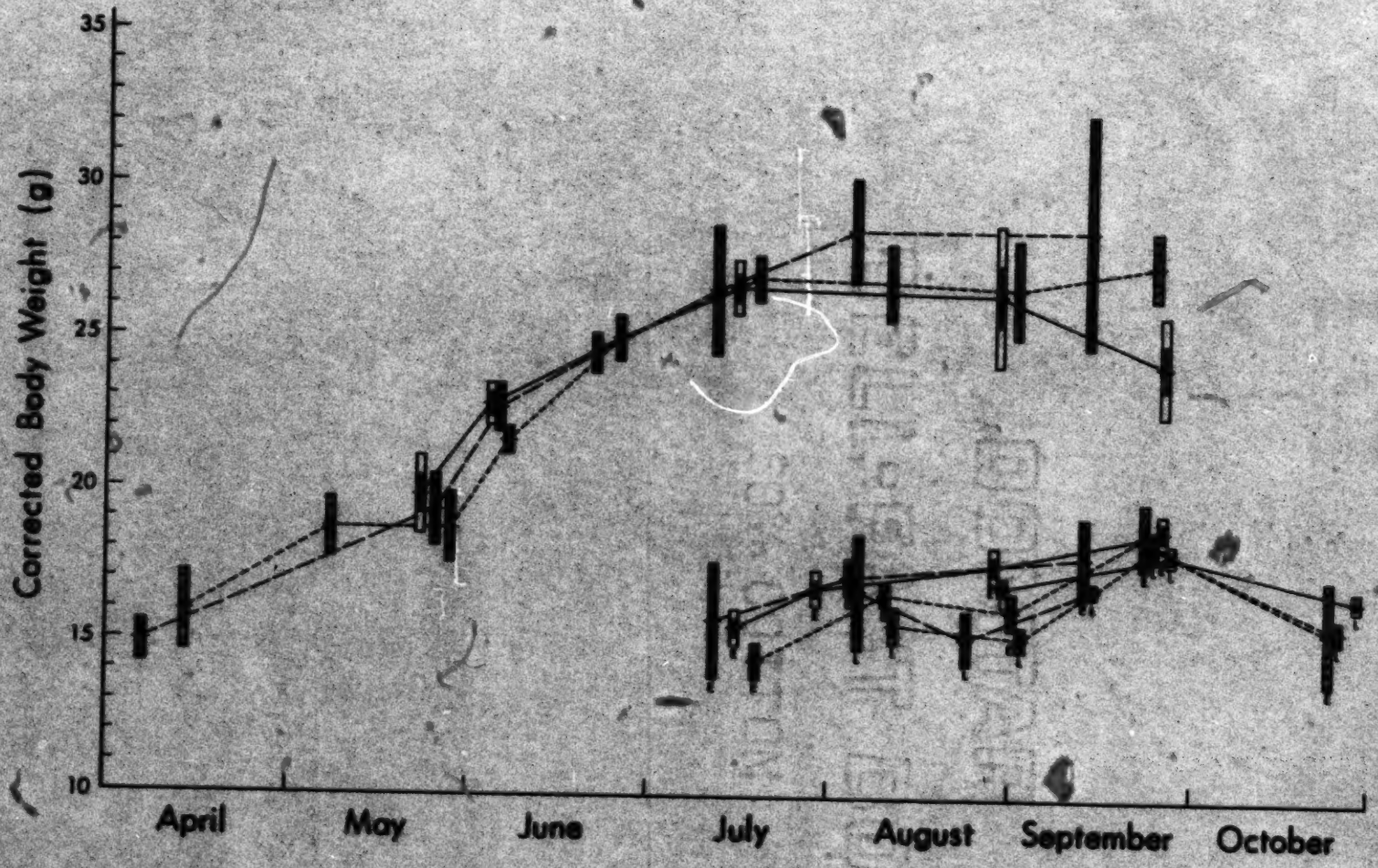

Figure 9. Corrected body weight of taiga animals 1971-1973. Symbols are the same as in Fig. 7.

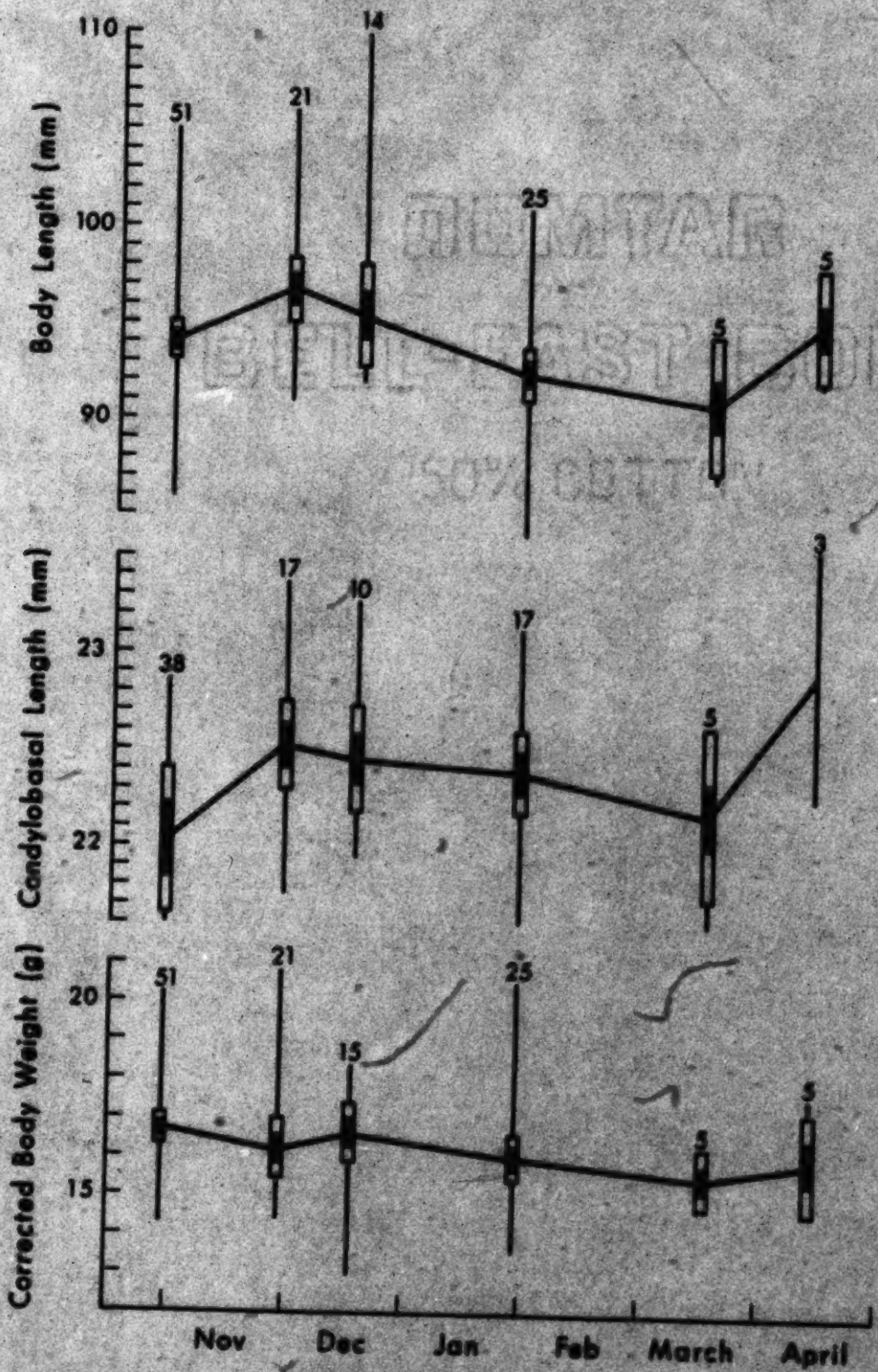

Figure 10. Body length, condylobasal length, and corrected body weight of taiga animals, sexes and age classes combined, during the winter of 1971-72. Mean ± SE ± 95% CL, range, and sample size are shown, except where the sample is less than 5.

added to the population. It was considered that the first litter of overwintered females was born from 1 June to 30 June and the second litter from 5 July to 5 September in 1971 and 1973 and from 10 June to 10 July and from 10 July to 10 September, respectively, in 1972. For litters born to early-cohort females, birth dates were assumed to be from 15 July to 5 September for the first litter and from 10 August to 5 September for the second. It was considered that young would not leave the nest until at least 15 days of age. A 1:1 sex ratio was assumed for all age classes and months.

The maximum number of young produced in each cohort was calculated by the following equation which assumes that half the pregnant females dying during the period when the litter is being born die before they give birth: $Y = (I_1\ B\ L) - \frac{1}{2}(I_1 - I_2)\ B\ L$

Where: Y = index of young produced

I_1 = index of females at time first young are born

I_2 = index of females at time last young are born

B = proportion of females breeding

L = number of viable embryos per breeding female

Only the contributions of overwintered and early-cohort females were calculated because that of late-cohort females was considered to be inconsequential. All of the early cohort were assumed to have entered the trappable population by 15-20 July and all of the late cohort by 20-25 September. There were no significant differences in disappearance between years for the early cohort or between 1971 and 1972 for the late cohort (Table 14). However, in 1973 more late-cohort animals were found in mid-September than was predicted. This suggests either that one of more of the parameters of the prediction equation were underestimated or

Table 14. A measure of disappearance in early and late cohorts based on the potential index and the observed index at a time when all of the cohort would be expected to have entered the trappable population. Significance of differences between years by X^2 test are indicated.

Year	Potential Index	EARLY COHORT 15-20 July Index	Disappearance
1971	13.14	3.64	72%
1972	5.06	1.63	68%
1973	3.05	0.61	80%
		(71,72,73) $p > 0.9$	

Year	Litter	Potential Index	LATE COHORT 20-25 Sept Index	Disappearance
1971	overwintered 2nd	5.63		
	early cohort 1st	3.10		
	early cohort 2nd	0.43		
	total	9.16	5.99	35%
1972	overwintered 2nd	2.34		
	early cohort 1st	1.17		
	early cohort 2nd	0.21		
	total	3.72	2.38	36%
1973	overwintered 2nd	1.04		
	early cohort 1st	1.85		
	early cohort 2nd	0.45		
	total	3.34	5.92+	
			(71,72) $p > 0.9$	

that the September population was overestimated. I was unable to determine which parameter (or parameters) was most likely incorrect.

At the onset of winter each year the population was composed of three age groups of animals: overwintered, less than 10%; early-cohort, about 10-15%; late-cohort, over 75%. Given a general winter decline in population level of 55-76% and equal loss between groups, a small number of overwintered and early-cohort animals could be present in the early summer trapping. In 1972 no overwintered animals were caught October III and in 1971 only one female was taken October III and none after that date. Overwintered animals trapped in September generally had very little crown left on their teeth and a few had only roots left. No animals with this degree of crown wear were taken in May or June of any year. These facts suggest that no animals successfully overwintered twice and that they may have disappeared early in their second winter.

I felt I could separate the two cohorts during the winter of 1971-72 on the basis of M2 root length (Fig. 11). The early cohort had longer roots because they formed earlier but both groups appeared to exhibit a similar growth rate. The distribution of M2 root lengths of overwintered animals June I of each year was plotted (Fig. 12). The general shape of the distributions was similar each year but the mean and range shifted. It is unclear from these distributions whether the shift was due to general differences in M2 root growth rates or to differences in the proportion of early-cohort animals in June I populations. A sample from Travaillant Lake*, approximately 105 km southeast of Inuvik, was used as a clue to the cause of the shift. The distribution of M2

*The sample was trapped late May-early June 1973 by N.W.T. Game Management Division personnel.

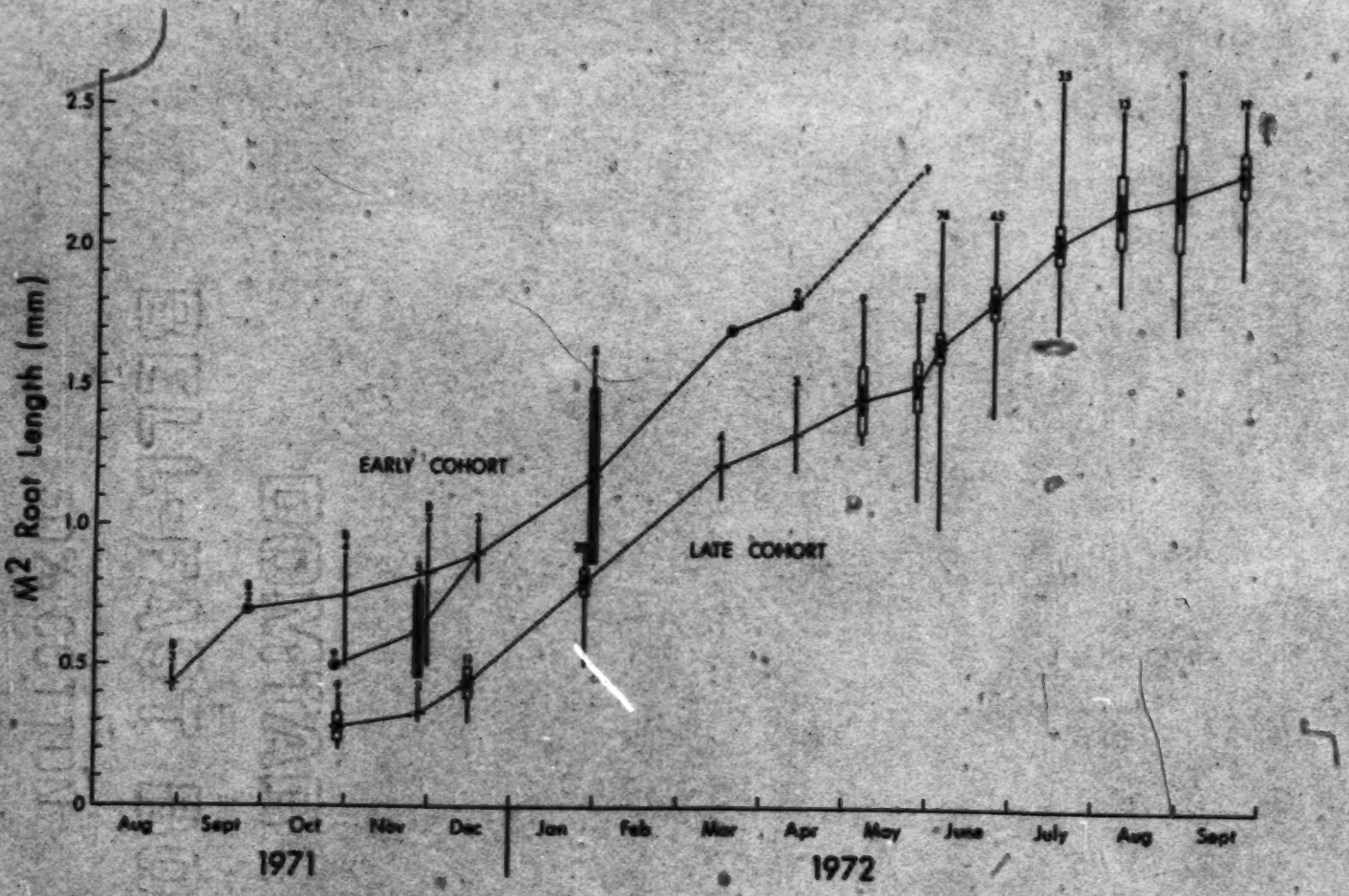

Figure 11. Length of second upper molar (M2) in 1971 early-cohort (bars) and late-cohort (open) animals (sexes combined). Early-cohort breeding individuals August-November 1971 are indicated by a "B" over the bar. Mean ± SE ± 95% CL, range, and sample size are shown.

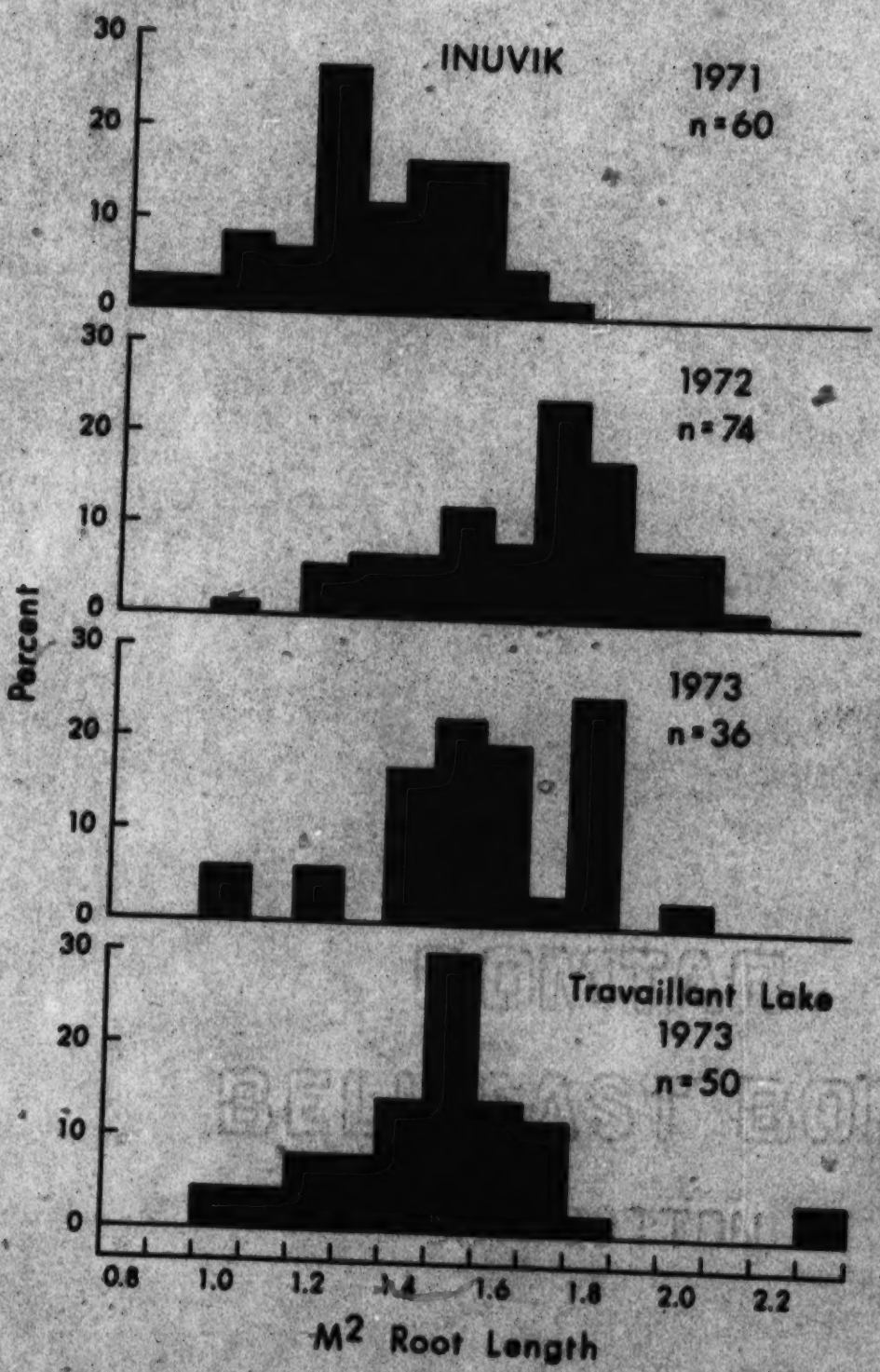

Figure 12. Distribution of M2 root lengths in early June samples at Inuvik, 1971-1973, and at Travaillant Lake in 1973.

root lengths of Travaillant Lake animals was clearly disjunct, and the mean and range of the larger portion of the sample was within the limits found at Inuvik.

I suggest, based on the 1971-72 winter M2 root growth (Fig. 11), that the two animals from Travaillant Lake, a male and a female, with 2.3 mm roots (significantly larger than the main group, t-test, $p < 0.001$), are the only early-cohort animals in this early summer sample. I also suggest that no early-cohort animals were present in the Inuvik samples and that the shift between years in the distribution of M2 root lengths was due to general differences in M2 root growth rates. Early-cohort animals, therefore, either disappear during their first winter or form an inconsequential part of the population during their second summer. Based on this, early-cohort animals seldom reach 12 months of age but late-cohort animals reach 13-15 months of age.

Assuming that only late-cohort animals overwintered successfully, a measure of their winter disappearance rate can be calculated from the population indices (Appendix 1). The winter (September III - June I) disappearance rate was 69% in 1971-72 and 42% in 1972-73.

Tundra Population

Population levels

An estimate of the variability of the population indices was calculated assuming that each of the 2-8 paired traplines run at each tundra site was an independent estimate of the population (Fig. 13). Population level July I was similar between years but may have been higher at snow-melt in 1971 than in 1972 or 1973. The summer increase was similar in 1971 and 1972 but was somewhat less in 1973. Winter declines can only

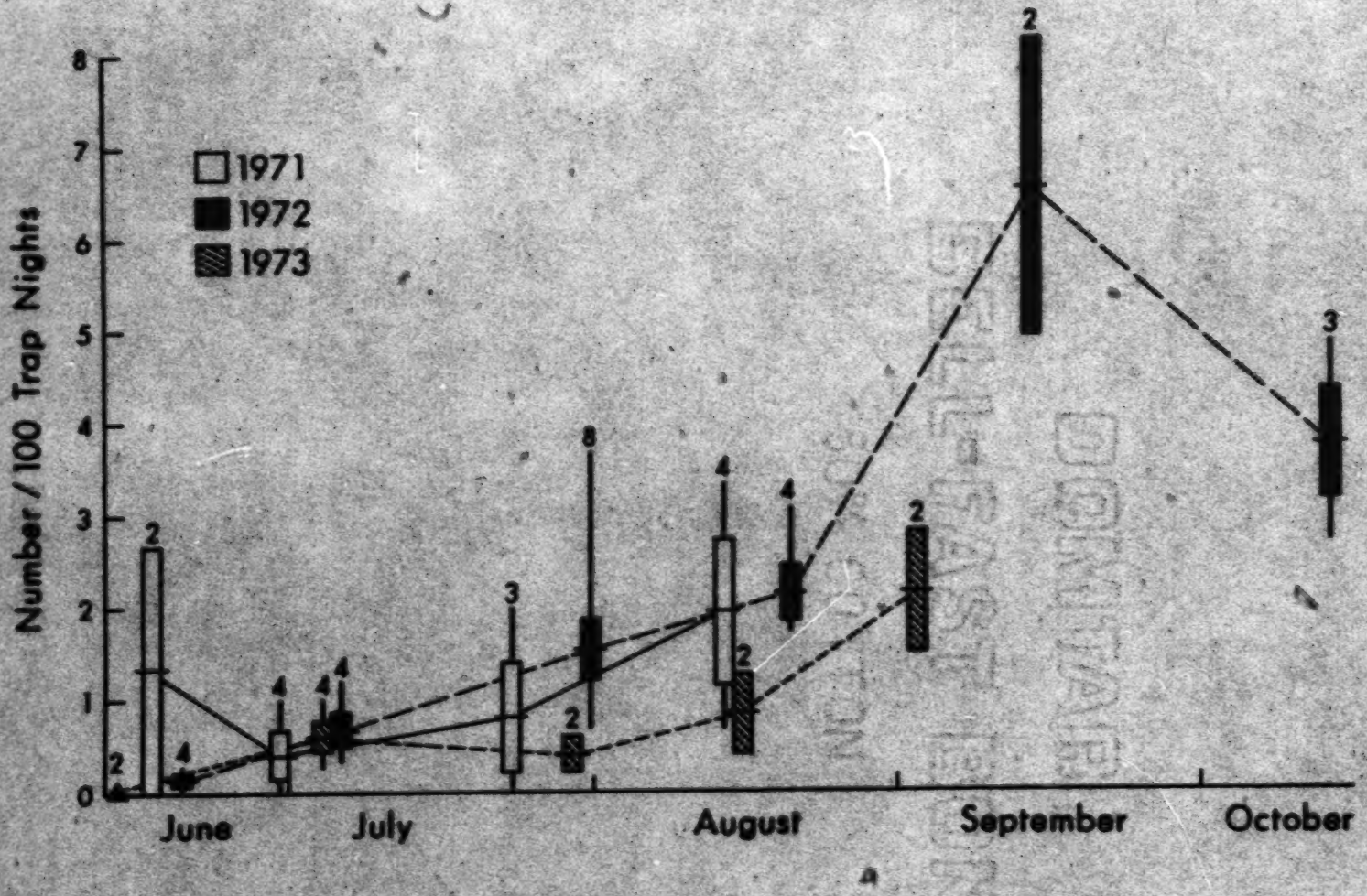

Figure 13. Tundra dead-trap indices (mean ± SE and range) based on 2 - 8 paired lines for each index.

be estimated but may have been 90-95%.

Because tundra areas were trapped in paired lines and taiga areas in grids, a greater number of home ranges were crossed on the tundra per unit effort and the edge effect was greater than in the taiga. Therefore, tundra indices are relatively higher than taiga indices for a given population density. At the beginning of summer, tundra population density was only a fraction of that in the taiga, even in the year of lowest taiga overwintered density, 1973. Peak density on the tundra in 1971 and 1972 may have been as high as or higher than that in the taiga in 1972 but was well below the levels reached in the taiga in 1971 and 1973.

Age structure

The distribution of birth dates of tundra litters (Fig. 15) is similar to that for taiga litters but is biased since the earliest tundra trapping was mid-June (after break-up of the Mackenzie River) and few animals were caught. Tundra litters were divided into two cohorts in the same manner as taiga litters. The representation of each age class in the population June-October 1971-73 is presented in Figure 14 and Appendix 11.

Sex ratio

Sex ratios of all dead-trapped animals caught during index trapping were examined (Table 15) and only a few significant differences from a 1:1 ratio were found. Mean sex ratio (proportion of males) of late-cohort animals was significantly smaller in 1973 than in 1972 (X^2 test, $0.01 > p > 0.001$); this was the only significant difference found between years in mean sex ratios of each age class.

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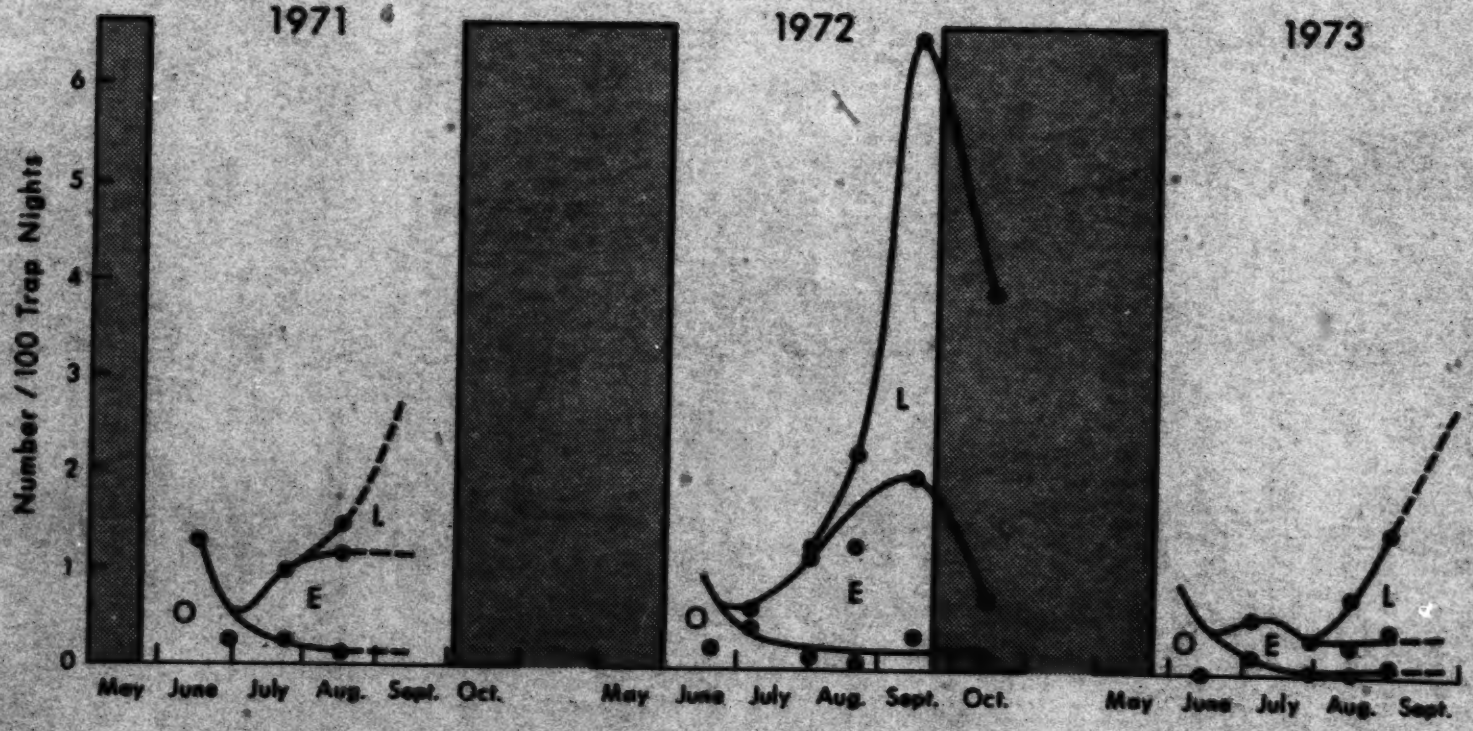

Figure 14. Tundra population indices showing the overwintered (O), early-cohort (E), and late-cohort (L) components. The periods of snowcover are shaded.

Table 15. Sex ratios (proportion of males) based on tundra index-trapping catches (sample size in parentheses) and compared to a 1:1 ratio by goodness of fit X^2.

Sampling period		1971		1972		1973	
				Overwintered			
June	II	.500	(4)	.333	(6)		
	III	.000	(2)				
July	I			.273	(22)	.417	(12)
	III	.500	(2)	.333	(9)	.000	(1)
Aug	II	1.000	(1)	.833	(6)	1.000	(1)
Sept	I					.500	(4)
	II			.167*	(12)		
Oct	II			.333	(3)		
Total		.444	(9)	.328*	(58)	.444	(18)
				Early cohort			
July	I			.500	(8)	.652	(23)
	III	.400	(5)	.533	(60)	.600	(10)
Aug	II	.714	(7)	.477	(65)	.556	(9)
Sept	I					.533	(15)
	II			.490	(51)		
Oct	II			.750	(16)		
Total		.583	(12)	.520	(200)	.596	(57)
				Late cohort			
July	III			.200	(5)	.000	(1)
Aug	II	1.000	(2)	.568	(51)	.533	(15)
Sept	I					.273**	(44)
	II			.524	(143)		
Oct	II			.557	(61)		
Total		1.000	(2)	.535	(260)	.333*	(60)

* $0.05 > p > 0.01$
** $0.01 > p > 0.001$

Mean sex ratio of each age class in each year was compared between tundra and taiga samples and three significant differences were found. Mean sex ratio of overwintered animals in 1972 and late-cohort animals in 1973 was significantly less on the tundra than in the taiga (X^2 test, $0.01 > p > 0.001$) and mean sex ratio of early-cohort animals in 1973 was significantly greater on the tundra than in the taiga (X^2 test, $0.05 > p > 0.01$).

Reproduction

Comparison of timing of litters between years was difficult due to small sample sizes (Fig. 15); however, there appeared to be no pronounced differences. In all three years 100% of overwintered females produced a first litter and an average of 92% of survivors to July II - October III produced a second litter in 1972 and 1973, with no significant difference between years (Table 16). An average of 58% of early-cohort females produced a first litter, with no significant differences between years (Table 17). In 1972 and 1973 an average of 35% of early-cohort females had a second litter, with no significant difference between years (Table 16). Pregnancy in late-cohort females was rare: 1.7% (2) of the females in 1972 and 1.3% (1) in 1973. There were no significant differences in litter size (Table 18) between litters, years, or age class of females (F test, $0.25 > p > 0.1$).

Overwintered males had functional testes June II - August II each year (Fig. 16). No regression was found September I 1973 but it had begun September II 1972. Males were still functional September II but not October II 1972. It was not possible to compare times of initial regression and loss of functional status between years.

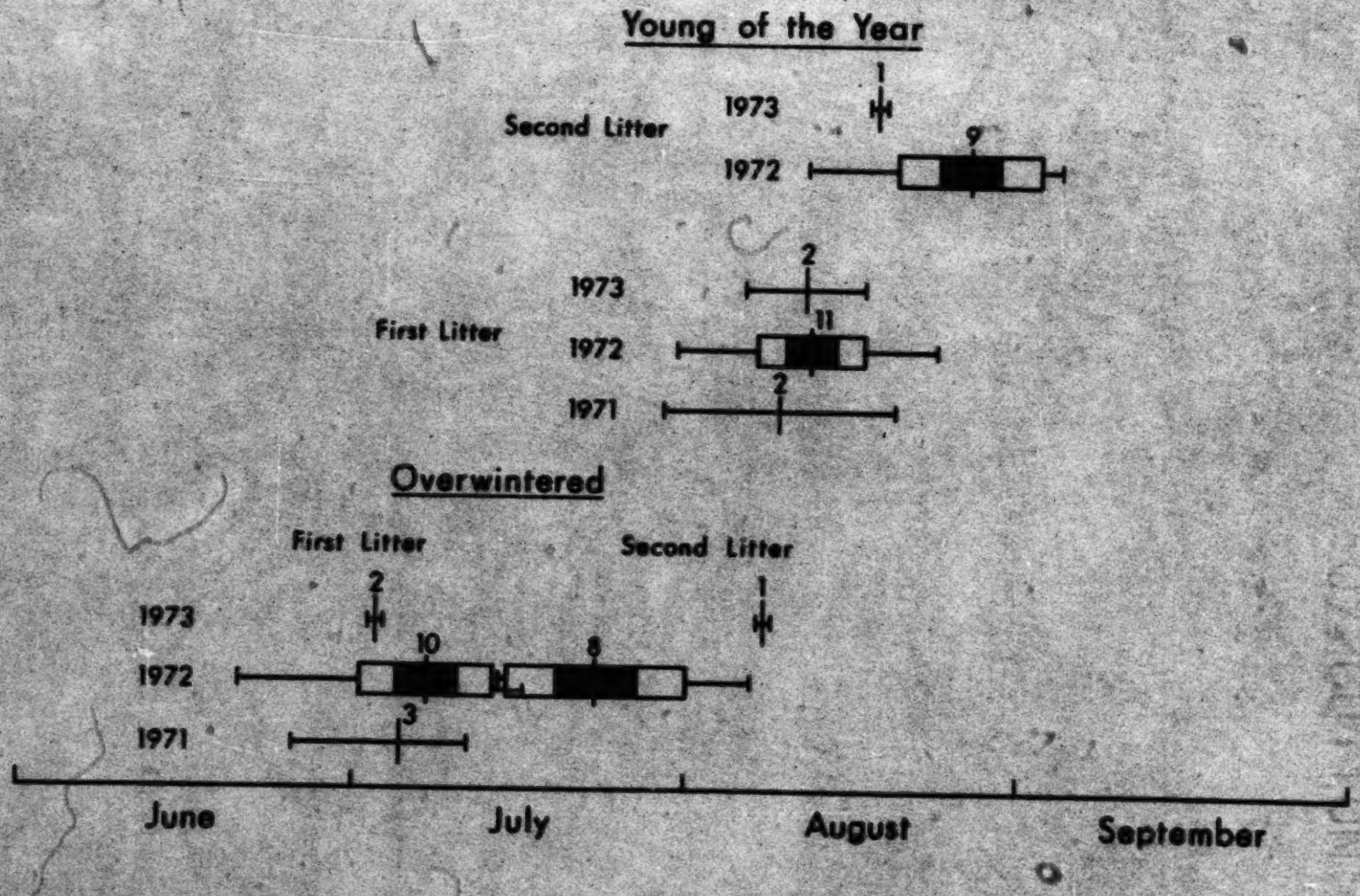

Figure 15. Birth dates for tundra litters based on embryo ages. Mean ± SE ± 95% CL, range, and sample size are presented in each case, except where the sample size is less than 5.

Table 16. Proportion of tundra breeding females captured July II-October III that produced a second litter, based on placental scar counts. Significance of differences between years by X^2 test is indicated.

Year	Overwintered %	Overwintered sample size	Early cohort %	Early cohort sample size
1972	94.7	(19)	32.4	(37)
1973	83.3	(6)	41.7	(12)
X^2 test	$0.5 > p > 0.1$		$0.9 > p > 0.5$	

Table 17. Proportion of tundra early-cohort females with embryos and/or placental scars. Significance of difference between July II-October III means by X^2 test is indicated.

Sampling period		1971		1972		1973	
July	I			0.0	(4)	0.0	(8)
	II						
	III	100.0	(3)	60.7	(28)	50.0	(4)
Aug	I						
	II	100.0	(2)	70.6	(34)	50.0	(10)
	III						
Sept	I					50.0	(14)
	II			34.6	(26)		
	III						
Oct	I						
	II			100.0	(4)		
	III						
Mean		100.0	(5)	58.7	(92)	50.0	(28)
X^2 test (71, 72, 73)		$0.5 > p > 0.1$					

Table 18. Tundra litter sizes, based on embryo count, and degree of resorption.

	First Litter				Second Litter			
		Total Count	Resorbing			Total Count	Resorbing	
Year	Sample size	Mean ± SE and Range	% Females	Mean no. of Embryos	Sample size	Mean ± SE and Range	% Females	Mean no. of Embryos
Overwintered								
1971	(3)	8.00 ± 0.000 (8)	33	0.67	(0)			
1972	(10)	7.90 ± 0.314 (7-10)	10	0.10	(8)	7.25 ± 0.453 (5-9)	0	
1973	(2)	8.00 ± 0.000 (8)	0		(1)	8.00 ± 0.000 (8)	0	
Early cohort								
1971	(2)	7.50 ± 0.500 (7-8)	0		(0)			
1972	(11)	6.82 ± 0.685 (2-11)	0		(9)	6.22 ± 0.494 (4-8)	11	0.11
1973	(2)	8.00 ± 1.000 (7-9)	0		(1)	9.00 ± 0.000 (9)	0	

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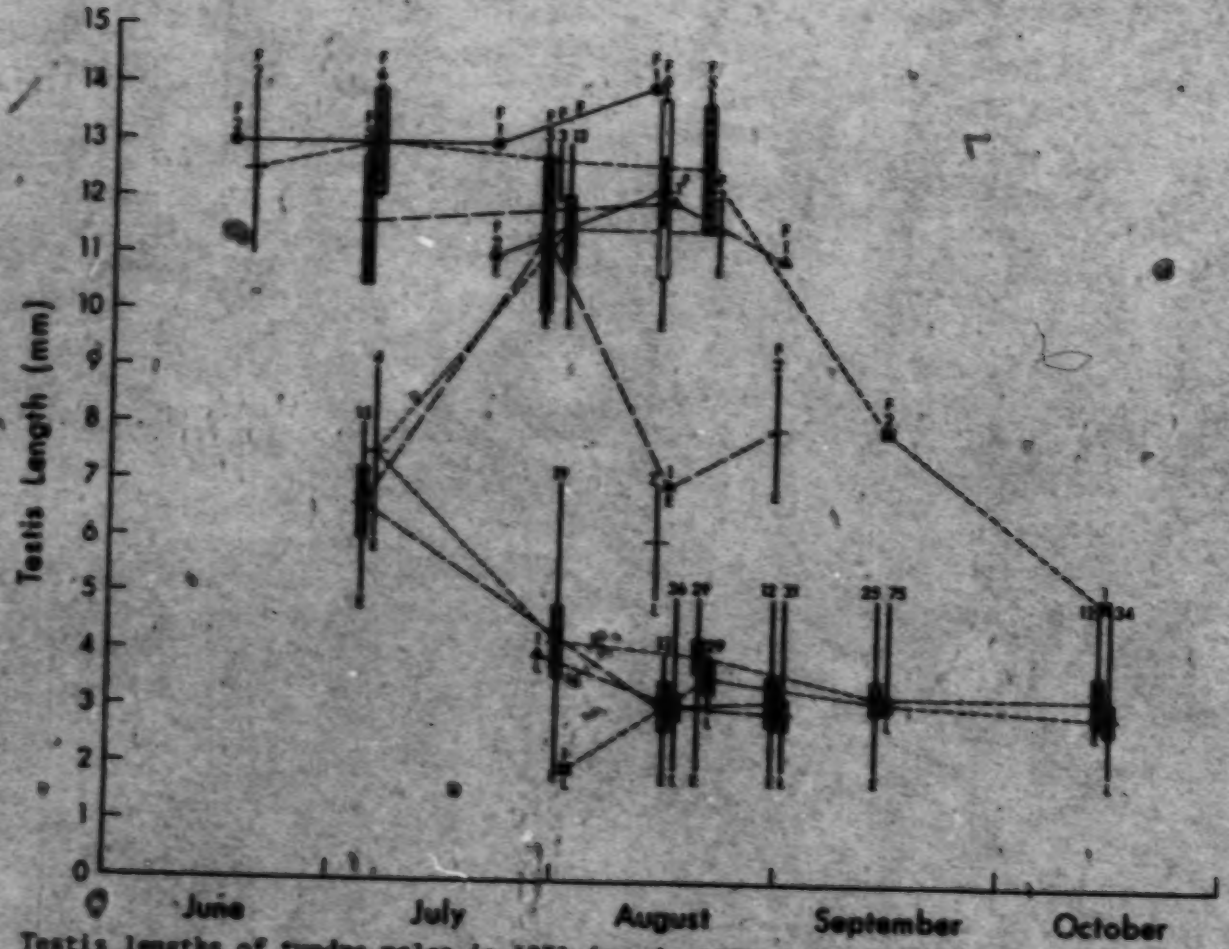

Figure 16. Testis lengths of tundra males in 1971 (open), 1972 (heavy bars), and 1973 (light bars). Early- and late-cohort males are designated by an "E" or "L" respectively below the bar; overwintered males have no mark below the bar. Functional males are indicated by an "F" above the bar. Mean ± SE ± 95% CL, range, and sample size are presented for samples of 5 or more; mean, range, and sample size are presented for samples of less than 5.

Breeding early-cohort males first became functional July II - III each year. They appeared to regress earlier in 1973 (August II) than in the other two years (probably late August or early September). An average of 28% of early-cohort males became functional in 1972 and 1973 but 100%, significantly more, did in 1971 (Table 19).

Participation in reproduction of early-cohort animals was compared between tundra and taiga for each year (Table 20). Significantly more early-cohort males became functional on the tundra in 1971 and 1972 than in the taiga but there was no significant difference in 1973. Significantly more early-cohort females produced a litter on the tundra in 1971 than in the taiga, significantly less did in 1973, and there was no significant difference in 1972. The proportion of overwintered and early-cohort females producing a second litter on the tundra was not significantly different from that found in the taiga (X^2 test, $0.9 > p > 0.5$ and $0.1 > p > 0.05$ respectively). Litter sizes were compared by litter and year between tundra and taiga. The first litter of overwintered animals was significantly larger on the tundra than in the taiga each year (t-test, $0.05 > p > 0.01$) but this was the only significant difference between the two areas.

Wounding

The frequencies of wounding on males and females in 1972 and 1973 (Appendix 12) were compared by age class in each year but no significant differences were found between sexes. No significant differences were found in the mean proportion wounded between 1972 and 1973 (Table 21).

The mean proportion with wounds was compared between tundra and taiga (Table 22). On the tundra, significantly more late-cohort males

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Table 19. Proportion of tundra early-cohort males functional. Significance of differences between July II-August III means by X^2 test are indicated.

Sampling period	1971 %	1971 sample size	1972 %	1972 sample size	1973 %	1973 sample size
June III						
I						
July II			0.0	(2)	0.0	(8)
III	100.0	(2)	40.6	(32)	83.3	(6)
I						
Aug II	100.0	(6)	6.4	(31)	7.7	(13)
III						
I						
Sept II			0.0	(25)	14.3	(14)
III						
I						
Oct II			0.0	(12)		
III						
Mean	100.0	(8)	23.8	(63)	31.6	(19)

X^2 test (71-72) $p < 0.001$
(71-73) $0.1 > p > 0.001$
(72-73) $0.5 > p > 0.1$

Table 20. Statistical differences (by X^2 test) between the mean proportion of tundra and taiga early-cohort animals breeding 1971-73.

		MALES		
		Tundra		
		1971	1972	1973
	1971	+ ***	+ **	+ **
Taiga	1972	+ ***	+ ***	+ ***
	1973	n.s.	n.s.	n.s.

		FEMALES		
		Tundra		
		1971	1972	1973
	1971	+ *	n.s.	n.s.
Taiga	1972	+ *	n.s.	n.s.
	1973	n.s.	- *	- *

n.s. (not significant) $p > 0.05$
* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $p < 0.001$
\+ proportion breeding greater on tundra than in taiga
\- proportion breeding less on tundra than in taiga

Table 21. Mean June-September proportion of tundra animals with wounds. Significance of differences between years by X^2 test are indicated.

Sex & Year	Overwintered %	Overwintered sample size	Early cohort %	Early cohort sample size	Late cohort %	Late cohort sample size
Males						
1972	11.1	(18)	9.8	(92)	7.6	(105)
1973	12.5	(8)	17.4	(46)	3.5	(57)
	n.s.		n.s.		n.s.	
Females						
1972	2.7	(37)	15.2	(92)	11.7	(94)
1973	0.0	(13)	13.9	(36)	6.5	(77)
	n.s.		n.s.		n.s.	

n.s. (not significant) $p > 0.05$

Table 22. Statistical differences (by X^2 test) between the mean June-September proportion of tundra and taiga animals with wounds.

		MALES tundra		FEMALES tundra	
		1972	1973	1972	1973
			OVERWINTERED		
	1971	- ***	- **	- *	n.s.
taiga	1972	n.s.	n.s.	n.s.	n.s.
	1973	n.s.	n.s.	n.s.	n.s.
			EARLY COHORT		
	1971	n.s.	n.s.	n.s.	n.s.
taiga	1972	n.s.	+ *	n.s.	n.s.
	1973	n.s.	n.s.	n.s.	n.s.
			LATE COHORT		
	1971	n.s.	n.s.	+ ***	+ *
taiga	1972	+ *	n.s.	+ **	+ *
	1973	+ *	n.s.	+ ***	+ **

n.s. (not significant) $p > 0.05$
* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $p < 0.001$
\+ proportion with wounds greater on tundra than in taiga
\- proportion with wounds less on tundra than in taiga

in 1972 and late-cohort females in 1972 and 1973 were wounded than were in the taiga. These were the only significant differences between areas when compared within years.

Organ weights

(i) adrenal

There were no marked differences between years in adrenal weights in any age-sex class (Appendix 13). Neither were there any marked differences in adrenal weights between tundra and taiga.

(ii) kidney

June - August kidney weights tended to be higher in 1972 than in 1971 or 1973; the latter two years were similar to each other (Appendix 14). Kidney weights on the tundra were similar to those in the taiga in early and late summer of each year; whereas mid-summer weights tended to be higher on the tundra than in the taiga, particularly in 1971 and 1972.

(iii) BAT

Interscapular BAT weights were similar between years in June and early July but later in the summer the values tended to be highest in 1971 and lowest in 1973 (Appendix 15). There were no marked differences in BAT weights between tundra and taiga.

Growth

Animals judged to be less than 25 days of age were eliminated from analysis. Mean body measurements (Appendices 16, 17, and 18) and the significance of differences between males and females (Appendix 19) are

presented in Appendices.

Body length (Fig. 17) tended to be greater in 1973 than in the other two years but no consistent differences were apparent in condylobasal length (Fig. 18) or body weight (Fig. 19). There were no consistent differences in body measurements between tundra and taiga.

Comparison of Live-trapped and Dead-trapped Samples

Density of *C. rutilus* on taiga and tundra live-trap plots (Table 23) is significantly correlated with the dead-trap index for similar time periods (correlation coefficient = 0.90, $p < 0.001$) and is related by the regression $y = 1.99x-1.14$. All live-trap densities were below 9/ha except that for 26-31 August 1971 which was almost 19/ha (Table 23). This high value excluded, live-trap density is significantly correlated with the dead-trap index (correlation coefficient = 0.92, $p < 0.001$) and is related by the regression $y = 1.33x+0.04$.

Age composition and sex ratios were compared between live-trapped and dead-trapped samples taken at similar times. No significant differences were found in age composition (Table 24), but live traps caught significantly more young males than dead traps July III and August III 1971 (Table 25). These were also the only two samples in which the live-trap sex ratios differed significantly from 1:1 (X^2 test, $p < 0.001$).

Weather

Introduction

For Inuvik and Tuktoyaktuk mean maximum and minimum temperatures by 10-day periods September 1970 to September 1973 and total precipitation

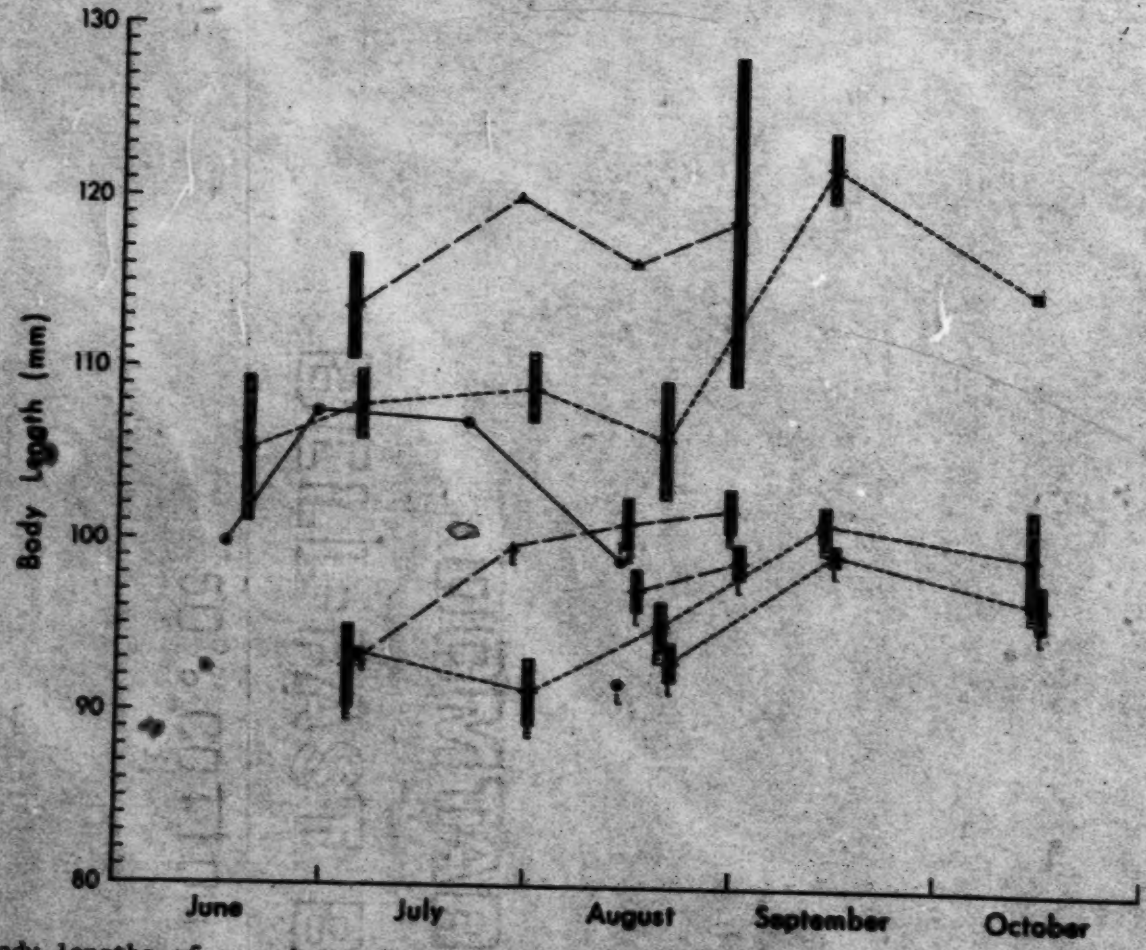


Figure 17. Body lengths of overwintered, early-cohort non-breeding (E), and late-cohort (L) tundra animals (sexes combined) in 1971, 1972 (heavy bars), and 1973 (light bars). Mean ± SE ± 95% CL are shown for sample sizes of 5 or greater; samples of less than 5 are shown as a point (1971, circle; 1972, square; 1973, triangle).

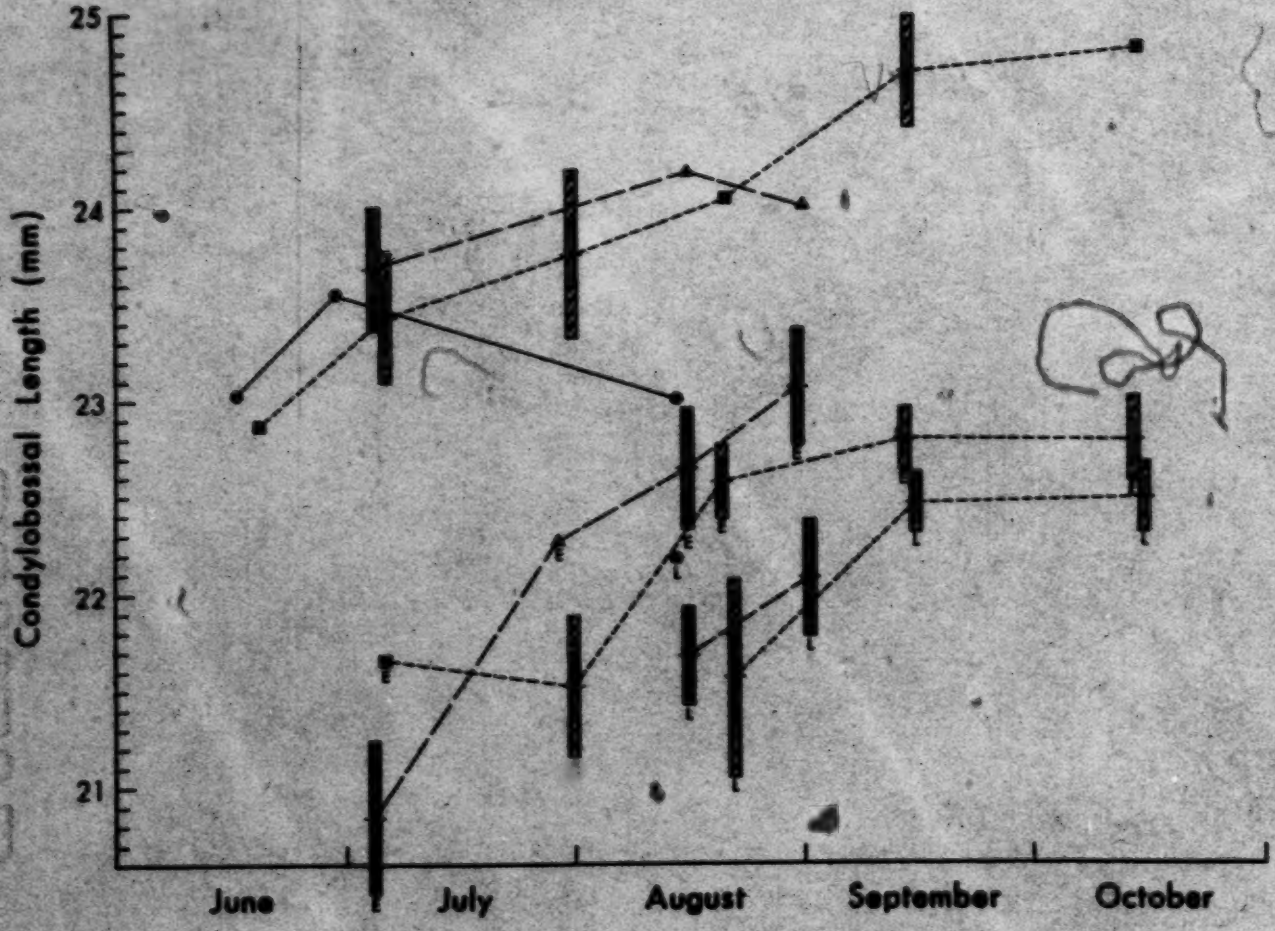


Figure 18. Condylobasal lengths of tundra animals 1971-1973. Symbols are the same as in Fig. 17.

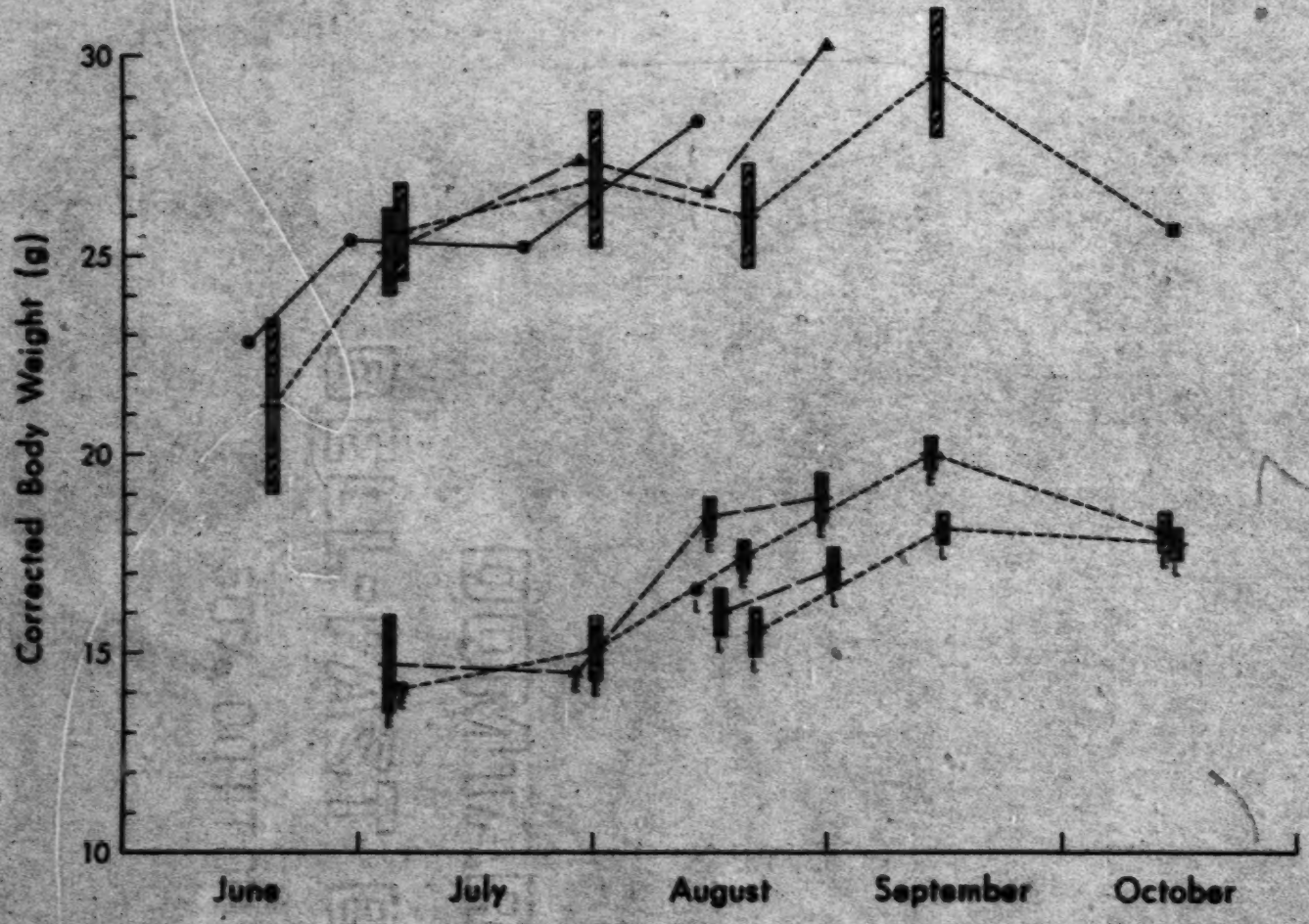


Figure 19. Corrected body weights of tundra animals 1971-1973. Symbols are the same as in Fig. 17.

Table 23. Density of *C. rutilus* (Number/ha) on taiga and tundra live-trap plots, 1971-1973.

Trapping Period	Spruce-Birch Forest	Spruce Forest	Shrub Tundra
1971			
May 28-June 18	4.00		
June 25-30			0.32
July 5-17	8.80		
July 17-29		8.64	
Aug 10-15			2.24
Aug 26-31	18.88		
1972			
June 12-27	2.72		
July 12-21		1.92	
1973			
June 10-18	1.76		
July 11-16		1.76	

Table 24. Age composition of live-trap and dead-trap samples. (sample size in parentheses.) Proportions are compared by X^2 test.

Sampling period	Method	Sample size	Percent Composition Overwintered	Young of the Year	Significance
TAIGA					
1971					
July II	Live	(55)	40.0	60.0	n.s.
	Dead	(63)	42.9	57.1	
July III	Live	(54)	22.2	77.8	n.s.
	Dead	(15)	13.3	86.7	
Aug III	Live	(118)	8.5	91.5	n.s.
	Dead	(164)	7.3	92.7	
1972					
July II	Live	(12)	33.3	66.7	n.s.
	Dead	(84)	41.7	58.3	
1973					
July II	Live	(11)	36.4	63.6	n.s.
	Dead	(24)	50.0	50.0	
TUNDRA					
1971					
Aug II	Live	(14)	7.1	92.9	n.s.
	Dead	(10)	10.0	90.0	

n.s. (not significant) $p > 0.05$

Table 25. Sex ratios (proportion of males) observed in live-trap and dead-trap samples (sample size in parentheses). Ratios are compared by X^2 test.

Sampling period	Method	Overwintered		Young of the Year		
TAIGA						
1971						
June I	Live	(25)	.560			
	Dead	(39)	.615			
July II	Live	(22)	.727	(33)	.485	
	Dead	(27)	.778	(36)	.417	
July III	Live	(12)	.417	(42)	.833	**
	Dead	(2)	.500	(13)	.462	
Aug III	Live	(10)	.700	(108)	.731	**
	Dead	(12)	.417	(152)	.559	
1972						
June II	Live	(17)	.529			
	Dead	(65)	.692			
July II	Live	(4)	.750	(7)	.571	
	Dead	(35)	.514	(49)	.592	
1973						
June II	Live	(10)	.500	(1)	1.000	
	Dead	(36)	.583			
July II	Live	(4)	.500	(7)	.428	
	Dead	(12)	.750	(12)	.417	
TUNDRA						
1971						
June III	Live	(2)	.500			
	Dead	(2)	.000			
Aug II	Live	(1)	.000	(13)	.769	
	Dead	(1)	1.000	(9)	.778	

** $0.01 > p > 0.001$

by 10-day periods May-September 1971-73 are presented in Appendices 20, 21, and 22. Comparison of depth of snow cover at Inuvik and Tuktoyaktuk can be obtained from snow-on-ground-at-end-of-month values (Appendix 23). This measurement is taken at only one point and is probably more unreliable at Tuktoyaktuk than at Inuvik because Longley (1960) observed that, for tundra areas, the depth of snow at any spot, after the initial increase in early winter, is a function of the ground surface contours in the vicinity and the direction of the last strong eroding wind. For Inuvik more accurate values are available from the snow cover survey (Appendix 24). The mean difference between the two surveys, compared on a monthly basis for the winters of 1970-71 to 1972-73, is 10.1 ± 1.6 cm with no significant differences either plus or minus.

Fall

Weather in September fell into three classes: (i) warm and dry (tundra 1971 and 1973, taiga 1973), (ii) cool and moist (tundra 1970 and 1972, taiga 1971), and (iii) cold and wet (taiga 1970 and 1972) (Fig. 20A). Fall critical period (FCP) is the period between the time when air temperature falls below that of the substrate and the time when a sufficient snow cover (15-20 cm) has formed to stabilize subniveam temperature (Pruitt 1957). An estimate of the severity of this period was made by comparing mean minimum temperature October II-III with depth of snow on the ground at the end of October (Fig. 20B). In order of increasing severity FCP's were (i) taiga 1971; (ii) tundra 1971 and 1972, and taiga 1972; (iii) taiga 1970; (iv) tundra 1970.

Fuller (1967) postulated that to be most favorable to small mammals fall should be dry with quick frosts and early stabilization of snow

Figure 20. Summary of weather data for taiga (solid) and tundra (open), 1970-73.

A. September: mean minimum temperature vs. total precipitation

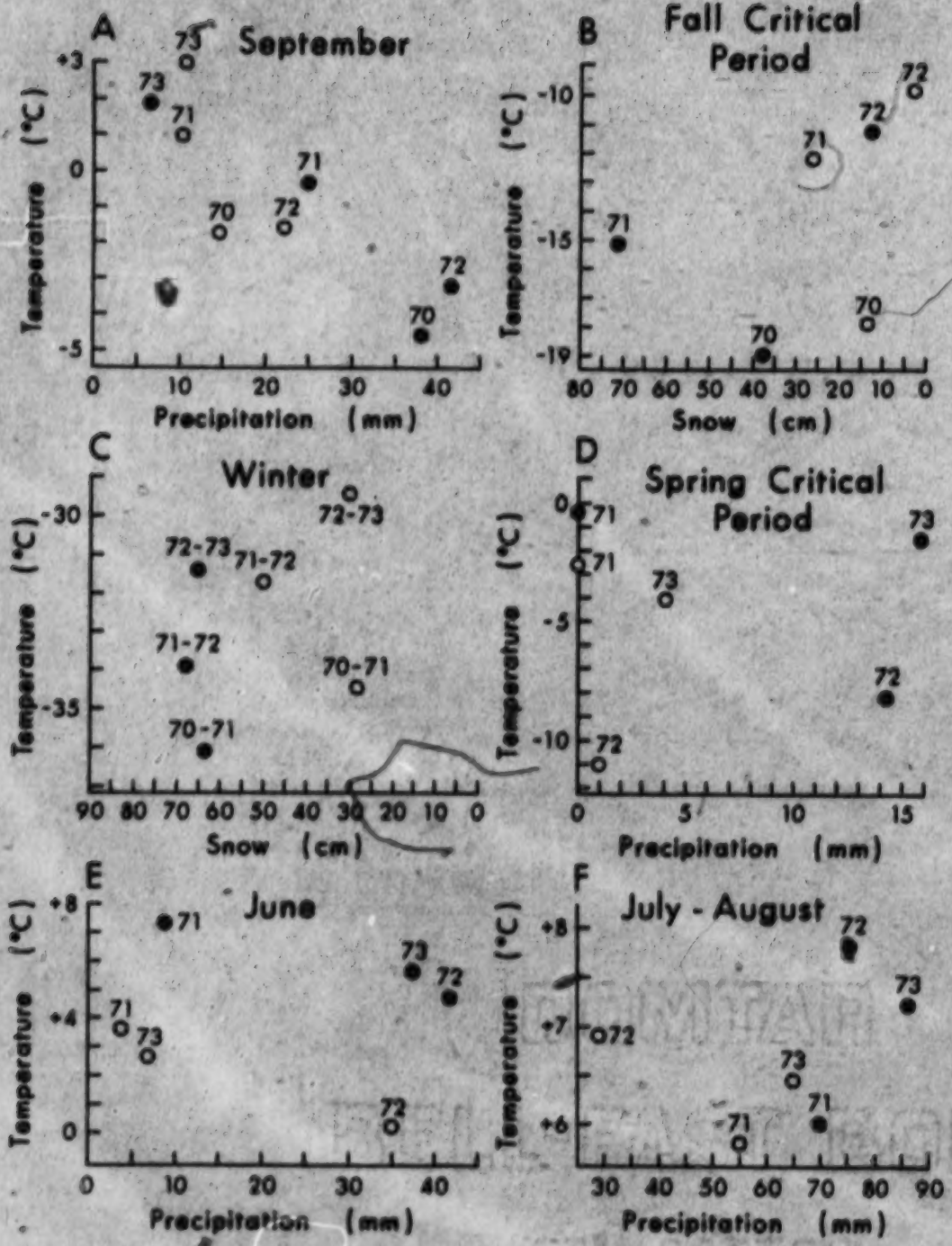
B. Fall Critical Period: mean minimum temperature October II-III vs. depth of snow on the ground at the end of October

C. Winter: mean minimum temperature December-March vs. mean depth of snow on the ground at the end of the month, December-March

D. Spring Critical Period: mean minimum temperature May II-III vs. total precipitation May II-III

E. June: mean minumum temperature vs. total precipitation

F. July-August: mean minumum temperature July-August vs. total precipitation July-August


A
September
Temperature (°C)
+3
0
-5
Precipitation (mm)
0 10 20 30 40
B
Fall Critical Period
Temperature (°C)
-10
-15
-19
Snow (cm)
80 70 60 50 40 30 20 10 0
C
Winter
Temperature (°C)
-30
-35
Snow (cm)
90 80 70 60 50 40 30 20 10 0
D
Spring Critical Period
Temperature (°C)
0
-5
-10
Precipitation (mm)
0 5 10 15
E
June
Temperature (°C)
+8
+4
0
Precipitation (mm)
0 10 20 30 40
F
July - August
Temperature (°C)
+8
+7
+6
Precipitation (mm)
30 40 50 60 70 80 90

cover. In this context the changeover from summer to winter conditions was most favorable in 1971 and least favorable in 1970. In each year conditions on the tundra tended to be better than those in the taiga.

Winter

In terms of mid-winter mean minimum temperatures, winters fell into four groups. In order of decreasing temperature they were (i) tundra 1972-73, (ii) tundra 1971-72 and taiga 1972-73, (iii) tundra 1970-71 and taiga 1971-72, and (iv) taiga 1970-71 (Fig. 20C). However, snow depths helped compensate for the lower temperatures in the taiga. Insulation of snow cover after mid-winter was similar between the winters of 1971-72 and 1972-73 but was much less on the tundra than in the taiga (Fig. 21). However, in the taiga, insulation was much better in early winter 1972-73 than in 1971-72 despite the greater snow depth 1971-72 (Appendices 23 and 24). This improved insulation was primarily due to the greater prevalence of wind in early winter 1971-72 which compacted the snow, thus reducing its insulating ability.

Fuller (1967) postulated that to be favorable to small mammals there should be sufficient snow cover to stabilize subnivean temperature. Taiga snow cover was similar all three winters and was probably sufficient to dampen fluctuations in air temperature and stabilize subnivean temperature (*cf.* Fuller *et al.* 1969, Johnson 1957, Pruitt 1957, Whitney 1973). Tundra snow cover was probably similar all three winters but offered less insulation and probably was insufficient either to maintain as high a subnivean temperature as found in the taiga or to stabilize subnivean temperature (*cf.* Fuller *et al.* 1975a, Kelley and Weaver 1969, MacLean *et al.* 1974, Pruitt 1957, Whitney 1973). Therefore, conditions

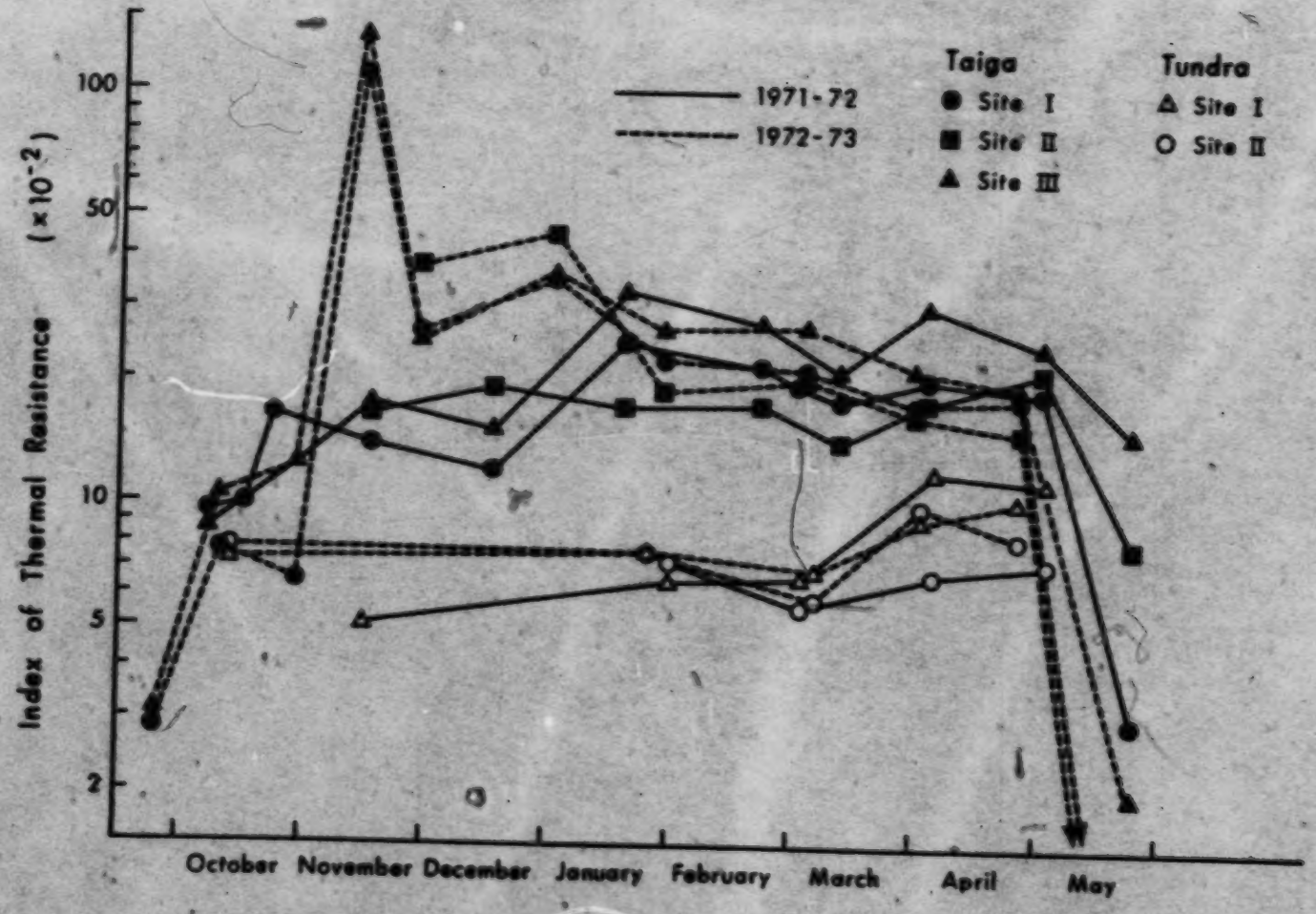


Figure 21. Tundra and taiga indices of thermal resistance for the winters of 1971-72 and 1972-73.

were much more favorable for small mammals in the taiga than on the tundra each winter, and may have been most favorable in the winter of 1972-73 and least favorable in 1970-71.

Spring

Spring critical period (SCP) is the period of active snow melt which marks the changeover from winter to summer conditions (Dunaeva 1948, Fuller 1967). Because snow cover is rapidly decreasing during May (Appendices 23 and 24), an estimate of the severity of SCP was made by comparing mean minimum temperature May II-III with total precipitation during the same period (Fig. 20D). In order of decreasing favorability, SCP was relatively (i) warm and dry on the tundra in 1971 and 1973 and in the taiga in 1971, (ii) cold and dry on the tundra in 1972, (iii) warm and wet in the taiga in 1973, and (iv) cold and wet in the taiga in 1972. Snowmelt was slowest in the taiga in 1972 (Appendices 23 and 24) and June I was relatively warm and dry in the taiga in 1971, intermediate on the tundra in 1971 and 1973 and in the taiga in 1973, and cold and wet both on the tundra and in the taiga in 1972 (Appendices 21 and 22).

Fuller (1967, 1969) postulated that to be most favorable to small mammals spring should be early, short, warm, and dry, with more sublimation than melting of snow. In this context, changeover from winter to summer conditions was (i) most favorable in the taiga in 1971, (ii) perhaps slightly less favorable on the tundra in 1971 and 1973, (iii) somewhat less favorable again in the taiga in 1973, and (iv) least favorable both on the tundra and in the taiga in 1972.

Summer

Tundra and taiga summer weather 1971-73 was evaluated based on the

assumption that cold, wet summer weather is detrimental to small mammals. In order of decreasing favorability, June weather was relatively (i) warm and dry in the taiga in 1971, (ii) cool and dry on the tundra in 1971 and 1973, (iii) cool and wet in the taiga in 1972 and 1973, and (iv) cold and wet on the tundra in 1972 (Fig. 20E). July and August varied much less in temperature than in precipitation but the weather was probably (i) best on the tundra in 1972; (ii) poorer on the tundra in 1971 and 1973, and in the taiga in 1971; and (iii) poorest in the taiga in 1972 and 1973 (Fig. 20F). In general, summer was (i) most favorable in the taiga in 1971, (ii) less favorable on the tundra in 1971 and 1973, and (iii) least favorable on the tundra in 1972 and in the taiga in 1972 and 1973.

In summary, 1970-71 combined the least favorable fall with the most favorable spring and summer in the taiga and with a less favorable spring and summer on the tundra, 1971-72 combined the most favorable fall with the least favorable spring and summer both on the tundra and in the taiga, and 1972-73 combined an intermediate fall with an intermediate spring and a poor summer in the taiga and with a slightly better spring and an intermediate summer on the tundra. All three winters were probably favorable in the taiga and less favorable on the tundra.

DISCUSSION

Trapping

One of the inherent problems of dead-trapping samples for population analysis is that the same sites cannot be re-trapped at close intervals without bias because the second sample is influenced by the removal of the first. To overcome this problem I trapped different

sites each time, being careful that each was, as well as I could tell, similar vegetationally and structurally, and representative of the area as a whole. Anderson (1970), however, has suggested that small mammals likely live in small, socially defined breeding groups (demes), some of which exist in the most favorable habitat types (survival habitat) and export their excesses to the less desirable areas (colonizing habitat) where mortality is higher. In favorable years the increased survival of animals in colonizing habitats may lead to a population high. This, then, raises a possible bias in my samples because I may have been sampling a different deme, or different demes, each time. Each deme, given intrinsic population control mechanisms, could be demographically different.

Myers (1974) studied two wild populations of *Mus musculus* but did not find a temporally stable demic structure. She also noted that populations of *Microtus pennsylvanicus* and *M. ochrogaster* which have been studied (Tamarin and Krebs 1969, Gaines and Krebs 1971) did not show genetic subdivision. It is quite possible then that the *C. rutilus* populations I studied do not exist in demes. However, this does not exclude the possibility that the proportions of survival and dispersal habitat with their quite different population types may have varied in each sample.

Proportions of survival and dispersal habitat would be expected to be influenced primarily by general habitat type and be reflected in population density, which has been observed to vary with habitat type in *C. rutilus* (Dyke 1971, Koshkina 1967a). Since taiga dead-trap areas are large (2-9 ha) and all were in similar forest types, they probably contained similar proportions of survival and dispersal habitat.

Therefore, taiga dead-trap samples were likely representative of the area as a whole.

Tundra dead-trap lines were sufficiently long to expect that many areas of survival and dispersal habitat were sampled at each site; also the general habitats sampled at each site were similar. Tundra dead-trap samples should, therefore, also be representative of the area as a whole, but the sites are so widely separated that local conditions probably have a greater effect on each sample than in the taiga.

A check on the possible bias of dead-trap samples was made by comparing them with live-trap samples taken at the same time. There was a significant correlation between dead-trap index and live-trap density, there were no significant differences in age composition of the two types of samples, and there were only two sampling periods in which a significant difference in sex ratio between the two types of samples occurred

The higher proportion of young males caught in live traps compared with snap traps July III and August III 1971 suggests that these animals were attracted differentially to the two types of traps. Both traps offer the stimulus of food as well as 'something-new-in-the-environment', but live traps also offer shelter. I suggest that young dispersing males were seeking shelter in July III and August III 1971, thus causing the high sex ratio. Young males have been shown to have a greater tendency to disperse than young females in *Microtus arvalis* (Frank 1966), *M. pennsylvanicus* (Van Vleck 1968), and *Peromyscus polionotus* (Smith 1968).

The close correlation between live-trap and dead-trap samples suggests that no significant differences were present between sites. Other studies have found correlations between catches from live-trap index lines and live-trap grids (Hansson 1967, Petticrew and Sadleir

1970) and dead-trap index lines and a live-trap grid (Yang *et al.* 1970). Petticrew and Sadleir (1970) also found similar survival rates and body weights in samples obtained by the two techniques and Yang *et al.* (1970) found no significant differences in weight classes or sexes caught.

Factors Affecting the Population

Extrinsic factors such as weather, food, predators, disease, and parasites may affect reproductive and mortality rates of a population. Because the role of weather is central to the hypothesis I set out to test, the majority of the discussion on the effects of extrinsic factors will relate to it.

To accurately appraise the role of food, detailed study of seasonal food usage, preference, availability, and quality is needed. Since this was considered beyond the scope of the study only qualitative and limited quantitative appraisals of relative food quantity were made. No marked differences in the abundance of berries between summers were detected. Also, a high percentage of the berries present in fall were still present the following spring, after snowmelt (*cf.* Dyke 1971). In a study of food in relation to fluctuating northern small mammal populations, Dyke (*Ibid.*) did not find any clear control exerted by food, although he suggested that food supply may have influenced the magnitude and pattern of numbers. I do not feel that differences in food supply either between tundra and taiga or between years were sufficient to produce the demographic differences observed.

Predators were not common in the study areas, although both avian and mammalian predators may have been more common on the tundra than in the taiga. The primary mammalian predator was probably red fox (*Vulpes vulpes*) as no signs of arctic fox (*Alopex lagopus*), marten

(*Martes americana*), or ermine (*Mustela erminea*) were encountered and signs of lynx (*Lynx lynx*) and wolf (*Canis lupus*) were rare. Avian predators were generally rare. Predation was not considered a significant mortality factor in this study.

No detailed studies were made on disease or parasites, except for stomach nematodes (*Mastophorus* and *Riotularia*), although all animals autopsied were examined qualitatively. No conspicuously diseased animals were found during the autopsies, and, in general, the same pattern and intensity of infection by stomach nematodes was found each year, both on the tundra and in the taiga (unpublished data). Disease and parasitism were not considered significant factors in population control in this study.

Extrinsic factors may cause demographic changes in a population either directly by altering mortality rates, or indirectly by modifying behavior and physiology. Changes in behavior and physiology may also result from interactions with other individuals of the same species. In the former case demographic changes brought about by proximally intrinsic factors - behavior and physiology - are ultimately extrinsic; in the latter case they are ultimately intrinsic. It is the role of these ultimately intrinsic factors which I will consider. Because I did not measure behavior and physiology directly, I will attempt to assess their role by monitoring their effects.

Effects of Extrinsic and Intrinsic Factors

Mortality rate

A general pattern was observed of overwintered animals disappearing by early in their second winter, early-cohort animals disappearing late

in their first winter or very early their second summer, and late-cohort animals making up the overwintered population in their second summer. This general pattern has also been reported for *C. glareolus* (Gliwicz *et al.* 1968, Kaikusalo 1972) and *C. rufocanus* (Fujimaki 1969, Kalela 1957), and suggested for *C. rutilus* (Sealander 1972).

Poor weather during the post-breeding, pre-winter period may affect the population directly by increasing mortality rate and/or indirectly by either weakening the animals and making them more susceptible to over-winter mortality or by decreasing the quality of the food supply needed by the overwintering population. The weather in September was most favorable on the tundra in 1971 and 1973 and in the taiga in 1973, less favorable on the tundra in 1972 and in the taiga in 1971, and least favorable in the taiga in 1972. A marked September decrease in population level occurred in the taiga in 1972 but not in the taiga in 1971 and probably not on the tundra in 1972 or in the taiga in 1973. This decrease was associated with an unusually cold, wet September and may have been due to an increase in mortality rate caused directly by weather.

Since overwinter mortality was measured by comparing the pre-FCP population level with the post-SCP population level both FCP and SCP will be considered along with mid-winter conditions in assessing the effect of winter weather on the population. An unfavorable FCP would be expected to affect the population directly through increasing mortality rate and/or indirectly through poor preservation of overwintering food supply. Adverse winter conditions and an unfavorable SCP would also be expected to affect the population through increased mortality rate.

The winter of 1971-72 had a much more favorable FCP and a much less

favorable SCP than the winter of 1972-73, both on the tundra and in the taiga. Mid-winter conditions were generally similar between years but may have been more favorable in 1972-73 than 1971-72. Conditions were also generally much more severe on the tundra than in the taiga. Over-winter mortality (1 October-1 June) was greater in the taiga in 1971-72 (76% of all animals; 69% of the late cohort) than in 1972-73 (55% of all animals; 42% of the late cohort) but was greater on the tundra (about 90-95% of all animals) than in the taiga both winters.

Fuller (1969) and Fuller *et al.* (1969), working just west of Great Slave Lake, N.W.T., reported a winter decline in *C. rutilus* populations of about 80% (100% of marked animals) in one winter and only 30% (47% of marked animals) the next. The high mortality in the former year was considered to have occurred in early March and to have been the direct result of exposure to a prolonged period of low temperatures from late December through early February. This period of low temperature was reflected in subnivean temperatures despite the fact that snow cover was greater that year than the following year; snow density was similar both years. Whitney (1973), working near Fairbanks, Alaska, found winter declines in *C. rutilus* of about 85% in a low snow winter and about 55% in a high snow winter. Subnivean temperatures were much lower and less stable during the low snow winter than during the high snow winter.

In my study, air temperatures in the taiga were lower during the winter of high mortality (1971-72) than during the winter of low mortality (1972-73) but I do not know if this was reflected in subnivean temperatures since no continuous readings of subnivean temperature were taken. In the taiga, the winter of 1971-72 was noticably less favorable than the winter of 1972-73 during SCP. I suggest that although low mid-

winter temperatures may have been partly responsible for the high overwinter mortality in 1971-72, the poor weather during SCP was also a factor.

A comparison of snow depths and air temperatures during the two winters with those of other studies suggests that subnivean temperatures were much higher and more stable in the taiga than on the tundra. Therefore, the higher overwinter mortality on the tundra may have been due to poor mid-winter subnivean conditions on the tundra.

Poor summer weather might increase mortality rates, particularly of young animals. A measure of mortality rate is available only for the taiga population. There was no significant difference between years in the summer mortality rate of overwintered animals although summer weather conditions were relatively more favorable in 1971 than in 1972 and 1973.

In order of decreasing favorability of June weather, the summers ranked as follows: taiga 1971, tundra 1971 and 1973, taiga 1972 and 1973, and tundra 1972. There was no difference in early-cohort mortality rate in the taiga despite the differences in weather conditions between years. In order of decreasing favorability of July-August weather, the summers ranked as follows: tundra 1972, tundra 1971 and 1973 and taiga 1971, taiga 1972 and 1973. Since there was no difference in late-cohort mortality in the taiga between 1971 and 1972 despite a difference in weather conditions, and because weather conditions were similar in 1972 and 1973, the possible decrease in late-cohort mortality rate in 1973 was probably not due to weather. It is also probable that there were no differences due to weather in early-cohort or late-cohort mortality rates between tundra and taiga in any year.

In the taiga the average disappearance for the early cohort was 75% over approximately 40 days (1971-73) and 35% for the late cohort over

approximately 50 days (1971-72); the late cohort disappearance rate may have been even less in 1973. For an island population of *C. glareolus* the disappearance rate for the spring cohorts was estimated to be approximately 45-48% over 43 days (Bujalska *et al.* 1968), 24-34% over 42 days (Petrusewicz *et al.* 1969/70), and 39-53% over 32-59 days (Ryszkowski and Truszkowski 1970) depending on the method of calculation. On the same island the disappearance rate for summer cohorts was estimated to be approximately 88-95% over 43 days (Bujalska *et al.* 1968) and 87-96% over 42 days (Petrusewicz *et al.* 1969/70). Ryszkowski (1971) studied *C. glareolus* in four forest types and found disappearance rates of 63-90% over 4-7 months for spring cohorts and 53-70% over 1-4 months for summer cohorts depending on the forest type. While the variability of these estimates is apparent and any comparisons must be made cautiously, it is clear that the disappearance rate of summer cohorts was much greater than that for spring cohorts in *C. glareolus*; while the reverse appears to be true for *C. rutilus* in my study. Adamczewska-Andrzejewska and Nabaglo (1974) also found higher early mortality rates for spring-born than for summer-born cohorts, in *Microtus arvalis*.

Precipitation was less in June and early July than in late July and August and temperatures tended to be either similar in both periods or somewhat warmer in the former. Therefore, one would expect that weather conditions would be more favorable in June and early July than in late July and August. The difference in mortality rates of the two cohorts does not appear to be related to environmental conditions.

Food is more available and perhaps of higher quality during the last half of the summer when new berries have become ripe than during the first half of the summer when only overwintered berries are found.

It is possible that the better nutritional base for nursing females and newly weaned young contributes to the increased survival of the late cohort.

Krebs *et al.* (1969), working on *Microtus* in southern Indiana, found that survival rates changed in a cyclic manner accompanying a cycle of numbers. Survival of both adults and juveniles was good during the increase phase but juvenile mortality increased during the peak and decline. Subadult and adult mortality, though staying low during the peak, increased during the decline. This general pattern has been found in other species of small mammals (Krebs 1964, Krebs *et al.* 1973, Krebs and Myers 1974).

In terms of a cycle in numbers, the taiga population in my study can be considered to have been in a peak phase in 1971, in a decline phase in 1972, and in an increase phase in 1973. There was no significant difference between phases in early-cohort mortality rate but late-cohort survival was probably better in the increase phase. There was no difference in mortality of overwintered animals between phases.

Sex ratio

In general, there were few significant departures from a 1:1 sex ratio and few significant differences in mean sex ratio of any age class between years. The most conspicuous difference between tundra and taiga occurred in 1973 when, in the taiga, the early cohort showed a deficiency of males and the late cohort showed an excess of males; on the tundra, the pattern was reversed. In the case of late-cohort animals, in the taiga the 1973 ratio was significantly greater than 1:1 and on the tundra it was significantly less than 1:1 and significantly smaller than in 1972.

Myers and Krebs (1971), working on *Microtus pennsylvanicus* and *M. ochrogaster*, found that resident populations showed a deficiency of males; whereas sex ratios of newly caught animals showed an excess of males. This was found to be due to decreased survival and increased mobility and growth of males rather than either a difference in sex ratio at birth or trappability. They found no consistent correlation between sex ratios and population parameters, using measures of density, rate of change in density, reproductive rate, and mortality rate, but noted a correlation between secondary sex ratio and maternal genotype in *M. ochrogaster*. The pattern I found may also have been due to differences in amount of dispersal between the populations or to a shift in maternal genotype during the summer.

Reproduction

Winter breeding (breeding under the snow other than immediately prior to snowmelt) in a number of small mammals has been associated with unusually favorable winter conditions (Sadleir 1969). During my study, only overwintered animals were encountered in early summer both on the tundra and in the taiga. Also, no indication of breeding was found in animals trapped during the winter of 1971-72.

Whitney (1973), working in central Alaska, reported two litters of *C. rutilus* born in metabolic chambers in late March and early April in a year with an unusually deep snow cover. Whitney's findings must be viewed cautiously because they are based on a live-trap plot where baited traps were left open at all times. This provided the animals with additional food and shelter and food supply has been related to winter breeding in *C. glareolus* (Zejda 1962, Andrzejewski 1974). The only

other reported case of winter breeding in *C. rutilus* is from the West Sayan Mountains, USSR (Khlebnikov 1970) where both pregnant and lactating females were captured in February after a favorable summer and autumn.

Fuller (1969) suggested that an unfavorable SCP might delay the onset of breeding. Since I was not able to sample tundra sites until mid-June, only taiga data are available for SCP. SCP in the taiga was relatively most favorable in 1971 and least favorable in 1972. Also, snowmelt was delayed a week to ten days in 1972 relative to 1971 and 1973.

Although there was little difference in dates of first conceptions between years, mean conception date for the first litter of overwintered females was delayed about 11 days in 1972 relative to the other two years. However, mean conception date of the second litter of overwintered females was delayed only about 5 days relative to the other two years; therefore, compensation was made for part of the initial delay.

First conception dates were similar between years but the mean date was delayed in the year with the most unfavorable SCP. This suggests that onset of breeding condition in females may be controlled by photoperiod, as has been proposed for *C. gapperi* in Alberta (Evernden and Fuller 1972) and *C. rutilus* in Alaska (Sealander 1967), but weather during SCP affects mean timing of production of young.

Fuller (1969) reported that onset of breeding in *C. rutilus* and *C. gapperi* was not "seriously" delayed in a year with an unusually late snowmelt but that intensity of breeding was reduced in the latter species. Therefore, mean birth date of the first litter of overwintered animals may have been delayed in *C. gapperi* if not in *C. rutilus*. A

delay in onset of breeding in a year with late snowmelt has also been reported for *C. rufocanus* (Koshkina 1957) and *Lemmus lemmus* (Koshkina and Khalanskii 1962) on the Kola Peninsula and *Peromyscus maniculatus* at Heart Lake (Fuller 1969), but this delay was compensated for later in the summer in the two species on the Kola Peninsula (Koshkina 1966a, Koshkina and Khalanski 1962).

Poor weather near the end of the potential breeding season might be expected to shorten the realized breeding season; whereas good weather might be expected to prolong it (Ashby 1967). In the taiga in 1971 and 1972 and on the tundra in 1972 the last conception took place in late August; whereas at least one female conceived in early September in the taiga in 1973. Overwintered males were still functional in the taiga in late September 1972 and on the tundra in mid-September 1972 but were not functional in the taiga in late September 1971 or mid-September 1973, although early-cohort males were functional in the taiga in mid-September 1973.

Weather in September was most favorable in the taiga in 1973, less favorable on the tundra in 1972 and in the taiga in 1971, and least favorable in the taiga in 1972. Favorable September weather may have permitted an extension of breeding season in taiga females in 1973 but there appears to be no correlation between September weather and length of breeding season in males.

Adverse summer weather might decrease the intensity of reproduction and/or the number of viable embryos per breeding female (Sadleir 1969). In general the summer weather was most favorable in the taiga in 1971, less favorable on the tundra in 1971 and 1973, and least favorable on the tundra in 1972 and in the taiga in 1972 and 1973. Although in the

taiga the most favorable summer occurred in 1971 and the least favorable in 1972 and 1973, significantly more early-cohort animals bred in 1973 than in 1971 or 1972. On the tundra there was no significant difference in the proportion of early-cohort animals breeding between years, despite the differences in weather. Also there was no significant difference in litter size or resorption rate between years, either on the tundra or in the taiga. The observed variations in summer weather were not associated with significant differences in intensity of reproduction or number of viable embryos per litter.

A decrease in reproductive output with an increase in population density has been shown for a number of small rodents (Sadleir 1969). Several causes of variations in reproductive output have been suggested. Christian (1971a) reviewed the relationship between population density and reproductive efficiency in a number of mammals and concluded that "endocrine or behavioral negative feedback mechanisms operate to increase mortality and decrease reproduction as density increases and can regulate and limit population growth if some other outside limiting factor does not do so first." Koshkina (1974a) found that for *C. rutilus* in the Salair taiga the intensity of reproduction of young-of-the-year was inversely correlated with the density of overwintering animals in spring. Krebs *et al.* (1973) and Krebs and Myers (1974) noted that cyclic variations in reproductive rate accompany cycles in numbers in several small mammals; reproductive rate varies from a maximum during the increase phase to a minimum during the decline. They suggested that this cyclic variation in reproductive rate has a genetic basis; while Schaffer and Tamarin (1973) noted that such cycles will occur with changes in population density if animals behave in such a way as to

maximize their Darwinian fitness. Variations in reproductive output in small rodents have also been related to length of breeding season (Mullen 1968), social factors such as territoriality (Bujalska 1970), and food quantity and quality (Kalela 1957, 1962; Koshkina 1957; Lack 1954; Sokolov and Baiagura 1974; Tast and Kalela 1971).

In the taiga, the highest population density was found in 1971 but there was no decrease in reproductive rate. There were no significant differences between years in either proportion of overwintered animals breeding or litter sizes, and there may have been no difference between years in the length of breeding season. However, in 1973, the year of lowest overwintered density in the spring, significantly more early-cohort males and females bred than in the other two years. This fits the pattern suggested by Koshkina (1974a). However, if 1973 is considered an increase phase and 1971 and 1972 peak and decline phases respectively, then the population also follows the pattern suggested by Krebs *et al.* (1973), Krebs and Myers (1974), and Schaffer and Tamarin (1973).

On the tundra, population density was relatively the same between years and overwintering densities were consistently lower than those in the taiga. There were no significant differences between years in either proportion of overwintered animals breeding or litter sizes, and there may have been no difference between years in length of breeding season. There was also no significant difference between years in proportion of early-cohort females breeding but a significantly higher proportion of early-cohort males were in breeding condition in 1971 than in 1972 and 1973. There was probably no difference between years in the number of litters/breeding female/breeding season. Since production depends on number of breeding females, litter size, and

number of litters/breeding female/breeding season there was probably no significant difference in production between years.

In 1971 and 1972 the proportion of early-cohort males breeding was significantly higher on the tundra than in the taiga but there was no significant difference in 1973. The proportion of early-cohort females breeding was significantly higher than that in the taiga in 1971, not different in 1972, and significantly lower in 1973. Considering both tundra and taiga animals, early-cohort males fit Koshkina's (1974a) hypothesis of high maturation rates at low overwintering densities but, clearly, females do not.

Wounding

Incidence of wounding is an index of intraspecific interactions and has been related to maturation and population density (Christian 1971a) and to phase of a population cycle (Chitty 1967). Krebs (1964) found a significant increase in the proportion of winter generation *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* with wounds in early summer of a high density ("peak") year; these differences were not significant late in the summer. He suggested that maturation of young male *Lemmus* in the summer of their birth leads to a great increase in fighting and that inhibition of maturation may be a mechanism to prevent fighting. Christian (1971b) found a significantly greater amount of wounding in mature male *Microtus pennsylvanicus* with increased population density but noted that immature males were seldom attacked, and then not severely. Krebs (1970) found from behavioral tests that *M. pennsylvanicus* and *M. ochrogaster* males were more aggressive in a high density peak phase than in lower density increase and decline phases.

In the taiga I found a much higher level of wounding in 1971 than in the other two years. Because population density was also greater in 1971 the increase in wounding appears to have been related to high density. This relationship is surprising as greatest density in 1971 was only about 11-19/ha.

Krebs' (1964) and Christian's (1971a) suggestion that maturation of young males in the year of their birth leads to a great increase in fighting was not supported in this study. Only in 1971 were significantly more mature than immature early-cohort animals wounded, but the greatest proportion of early-cohort animals maturing in the year of their birth was in 1973. The level of wounding in early-cohort animals was better related to population density than to maturation.

Significantly more late-cohort males and females in 1972 and late-cohort females in 1973 were wounded on the tundra than in the taiga. This does not appear to be related either to density or to maturation because density was generally lower on the tundra than in the taiga and maturation of late-cohort animals was rare in both areas. However, assuming that suitable overwintering habitat is more restricted on the tundra than in the taiga, the higher incidence of wounding in late-cohort tundra animals may be the result of more intensive intraspecific competition for suitable winter habitat.

Testis length

In the taiga, the June-August testis length in overwintered males was significantly less in 1973 than in 1971 and 1972. Mullen (1968) found significantly longer testes in *Lemmus trimucronatus* during a year of "high" density than in the following two years of much lower density.

In Mullen's "peak" year the population density was highest in June and declined rapidly during the summer; while in my study, in 1973 a low density population in June increased rapidly towards the end of the summer. These data suggest that testis length is related either directly to density, to density and to the rate of summer increase of the population, or to the phase in a cycle of numbers. In any case, the biological significance of the relationship is obscure.

An alternate solution is offered by Bodenheimer's (1949, cited by Sadleir 1969) work on wild populations of *Microtus guentheri*. His study suggested that an increase in the level of available nutrition caused an increase in testis size. This does not appear to have been a likely factor in my study because an unusually low level of food availability would not be expected to accompany the significant increase in productivity observed in 1973. Nor does it appear to have been a factor in Mullen's study because the level of available nutrition (pounds of protein per acre) was lower in the peak year than in the year following the peak (Mullen 1968).

Organ weights

(i) adrenal

Changes in adrenal weight and/or pituitary-adrenocortical function connected with changes in population size have been shown in both laboratory and field (Christian 1971a). However, in wild populations, some inconsistencies occur (Andrews 1970) and some reported density differences (Christian and Davis 1966) can be explained by a seasonal pattern.

The only significant difference in adrenal weight either

between years or between tundra and taiga occurred May III in the taiga when both overwintered males and females in 1971 had heavier adrenals than in the other two years. Because these heavy weights occurred during the peak of the spring breeding season in the year with highest overwintered population density, it is possible that the increase was directly related to density. Adrenals in late-cohort taiga animals tended to be heaviest in 1973 and lightest in 1971, showing no direct relationship with population density. In general, no consistent relationship between adrenal weight and population density was found.

(ii) kidney

Soviet workers (Schwartz 1963, Schwartz *et al.* 1964) have noted that kidney weight is an index of general metabolic rate; the conditions which favor intensification of metabolism are accompanied by an increase in relative kidney weight and a decrease in metabolic rate is accompanied by a decrease in relative kidney weight. Kidney weight in *C. rutilus* has been reported to follow an annual cycle, with higher weights in summer than in winter (Sealander and Bickerstaff 1967). This fluctuation was considered to be related to ambient air temperature (*Ibid.*), but perhaps is better related to general environmental conditons. It was anticipated that variations in kidney weight between years or areas might serve as an index of the relative environmental conditions experienced by the voles.

In the taiga, a marked decrease in kidney weight occurred

during FCP in 1971 but not in 1972 when environmental conditions were less favorable. If the decline in 1971 is considered part of the normal decline from summer to winter kidney weights, then the adverse conditions during FCP in 1972 may have required the animals to have a higher metabolic output than in 1971, thus delaying the normal decline and resulting in higher October III kidney weights in 1972 than in 1971.

April kidney weights in the taiga were higher in 1973 than in 1972. If the animals reacted to unfavorable winter conditions by decreasing their general metabolic rate, then the differences I found in April kidney weights indicate that subnivean conditions were more unfavorable in 1971-72 than in 1972-73. Climatic data support this suggestion because air temperatures in mid-winter and in late March and early April were lower in the winter of 1971-72 than in 1972-73. In the taiga, environmental conditions during SCP were best in 1971 and poorest in 1972. However, little difference between years was apparent in May III - June I kidney weights, although they tended to be highest in 1971 and lowest in 1973. Environmental conditions during SCP did not appear to have a pronounced effect on kidney weight.

Early and late summer kidney weights were relatively similar both between years and between tundra and taiga. However, early summer weights tended to be highest in 1971 and lowest in 1973; while late summer weights tended to be higher in 1972 than in the other two years. The greatest differences were found in mid-summer. In decreasing order, mid-summer weights

ranked as follows: (i) tundra 1972, (ii) taiga 1972, (iii) tundra 1973 and taiga 1973, (iv) tundra 1971, (v) taiga 1971.

Environmental conditions in June varied greatly between years and areas and, in general, tended to be best in 1971 and poorest in 1973. Environmental conditions in August also varied greatly between years and areas and tended to be best on the tundra in 1972 and poorest in the taiga in 1971. In both early and late summer there was little variation in kidney weights despite wide variation in environmental conditions. However, early and late summer kidney weights did reflect environmental conditions to some extent; weights were lower when environmental conditions were poorer and higher when conditions were better.

Environmental conditions in July varied much less than those in June or August but were probably best on the tundra in 1972 and in the taiga in 1971 and 1972, poorer on the tundra in 1971 and 1973, and poorest in the taiga in 1973. There was no correlation between mid-summer kidney weights and environmental conditions in July.

Although kidney weight followed an annual fluctuation with low weights in winter and high weights in summer, the differences between years and areas, in spring and summer, were not well correlated with environmental conditions. It is possible that the physiological state of the animal is more influenced by reproduction and other intraspecific interactions during these periods than by weather. Kidney weight, therefore, was not considered a sensitive or consistent index of environmen-

tal conditions experienced by the animals during spring and summer.

In fall and winter, however, the physiological state of the animal may be more affected by environmental conditions than in spring and summer; hence the closer correlation found during this period. Fall and winter kidney weights may, therefore, serve as an index of the environmental conditions experienced by the voles. Based on this index, FCP in 1972 and the winter of 1971-72 were environmentally more unfavorable for voles than FCP in 1971 and the winter of 1972-73.

(iii) BAT

Brown adipose tissue (BAT) is known to be a thermogenic effector organ in mammals (Smith and Horwitz 1969), and Didow and Hayward (1969) demonstrated that in a natural population of *Microtus pennsylvanicus* relative BAT weight was related to the seasonal requirement for cold thermogenesis. Didow and Hayward (*Ibid.*) also suggested that thermogenic mechanisms are most important in thermoregulation of voles during the cold exposure of late autumn and early winter.

Annual cycle of BAT weight has been studied in several species of small mammals including *C. rutilus* (Scalander 1972) and some workers have found interannual differences (Didow and Hayward 1969, Meumier 1969, Pasanen 1971). Interannual differences in BAT weight should be related to the interannual differences in environmental conditions experienced by small mammals. Therefore, interscapular BAT weight should serve as an index of these conditions.

In the taiga there was no difference in BAT weight during FCP between 1971 and 1972 despite the difference in environmental conditions. There was also no difference in BAT weight during late winter and SCP between 1972 and 1973, again despite the difference in environmental conditions.

Early summer BAT weight in the taiga tended to be higher in 1971 than in the other two years and late summer BAT weight both on the tundra and in the taiga tended to be highest in 1971 and lowest in 1973. Early summer (June) environmental conditions were better in the taiga in 1971 than in 1972 or 1973, and late summer (August-September) conditions in order of increasing severity were as follows: tundra all years, taiga 1971, taiga 1973, taiga 1972. The expected correlation between high BAT weight and severe environmental conditions was not present. Interscapular BAT weight was not considered a sensitive indicator of the environmental conditions experienced by the voles.

Growth

Hyvärinen and Heikura (1971) postulated that the annual pattern of growth in *C. glareolus* and *C. rutilus* was partially controlled by a seasonal endogenous rhythm but noted that winter environmental conditions or population density may modify the pattern. A general pattern of decline in body weight from October to November, a relatively stable level from November to February and an increase beginning in March has been demonstrated for three populations of *C. rutilus* (Boikova and Boikov 1972, Fuller *et al.* 1969, Sealander 1966). The same pattern was

reflected in condylobasal length in one of the populations (Boikova and Boikov 1972) but no significant change in body length from October to March was found in another (Stebbins 1968).

I observed a significant decline in body weight in late-cohort taiga animals in October 1971 and 1972 and in early-cohort tundra animals in October 1972. October declines also occurred in early-cohort taiga animals in 1971 and 1972 and late-cohort tundra animals in 1972 but were not significant. No further significant changes in body weight of young-of-the-year occurred October III 1971 through April II 1972. Condylobasal length and body length of taiga young-of-the-year showed some increase through November 1971, a decrease to mid-March 1972, and an increase after mid-March; but these differences were generally not significant.

Fuller *et al.* (1969) suggested that a decrease in mean body weight in winter occurs in most, if not all, Holarctic microtines and is brought about by three processes: death of oldest (largest) animals, cessation of growth in the youngest, and an actual decline in weight of those older animals that survive. The decrease in body length and condylobasal length observed in my study can probably be attributed to the first two processes suggested by Fuller *et al.* However, the October decline in body weight was not restricted to older animals; it occurred in both breeding and non-breeding early-cohort, and late-cohort individuals. This suggests that early winter declines in body weight occur on an individual level and are not artifacts of a changing age structure of the population. Winter weight losses at an individual level have also been reported in *Microtus pennsylvanicus* (Iverson and Turner 1974). As has been pointed out by several workers (Boikova and Boikov 1972,

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Puller *et al.* 1969, Kalela 1957, Mezhzherin 1964) this weight loss is probably a cold climate adaptation, at least in subnivean mammals, and the advantage lies in a decrease in overall energy requirements.

Hyvärinen and Heikura (1971) observed in *C. glareolus* that growth was more severely retarded and bone alkaline phosphatase activity was lower in a winter of "very high" population density than in a winter of lower population density and "better living conditions." The October decline in body weight in late-cohort taiga animals, in my study was significantly greater in 1972 than in 1971. This may have been related to FCP, which was more severe in 1972 than in 1971.

Puller (1969) suggested that an unfavorable SCP might delay weight gain in overwintered animals. He found that weight of overwintered *C. gapperi* and *P. maniculatus* in May was significantly less in a year with an unfavorable SCP, and that *C. gapperi* females weighed significantly less than males during that May. Puller suggested that the low weights were caused by the late spring - the animals were unable to secure sufficient energy to add weight in addition to the extra thermal stress, females being more severely affected than males. At the same time, however, he did not find these trends in *C. rutilus*, which was postulated to have a greater cold tolerance than *C. gapperi*.

Although, in my study, the mean body weight of both overwintered males and females in the taiga May III - June I was less in 1972 (least favorable SCP) than in the other years, this difference was not significant. As in Puller's study, spring weight gain in *C. rutilus* was not significantly affected by conditions during SCP. Females weighed significantly less than males in May III each year and in June I, 1972, but, in general, there were no significant differences later in the

summer. Spring weight gain in females is probably delayed relative to that in males due to the energy demands of pregnancy.

In the taiga, summer growth in body length was significantly less in 1971 than in 1972 or 1973. This trend was also apparent in condylobasal length but not in body weight. Zejda (1971) noted that growth is better characterized by body length than by body weight, a fact which may help account for the lack of difference in weight between years.

Summer weather was more favorable in 1971 than in the other two years. The retardation in growth, therefore, does not appear to be related to weather. Food quality may have been a factor but, because it was not measured, its role cannot be assessed.

Koshkina (1957) found that in high density populations of *C. glareolus*, growth of young stopped early and young had lower weights in fall than in years with lower densities. However, this may have been related to the proportion of young maturing because: (i) young that mature in the year of their birth grow more rapidly than those that remain immature (Bujalska and Gliwicz 1972, Kalela 1957, Zejda 1971), and (ii) fewer young mature in the year of their birth in high than in low density populations (see Sadleir 1969). The generally reduced growth in the taiga in 1971 in my study also occurred in a high density population but was found in each age class and was not an artifact of differential maturation rates. If maturation was not involved in Koshkina's study then both populations may have shown a decreased growth rate with high population density.

Krebs *et al.* (1969) found higher individual growth rates in increasing populations of both *Microtus pennsylvanicus* and *M. ochrogaster* than in peak populations, which in turn had higher rates than

50% COTTON

declining populations. Increasing and peak populations of several microtines have been characterized by adults of large body size (weight) which are eliminated in declining populations (Chitty and Chitty 1962; Fuller *et al.* 1975b; Kalela 1957; Keller and Krebs 1970; Krebs 1964, 1966; Krebs *et al.* 1969). These variations in growth rate and body size have been considered to change in a cyclic manner accompanying the cycle of numbers and to have a genetic basis (Krebs *et al.* 1973, Krebs and Myers 1974).

In my study there was no significant variation in body weight either between years or between areas, despite marked changes in population density. However, animals tended to be heavier in relation to body length in the taiga in 1971, but body length was shorter than in the other two years. If this effect were genetic it would not be expected to occur in both parents and offspring in one summer (1971) but not be apparent in the offspring in their second summer (overwintered animals in 1972). It is more likely that some other factor (food, aggression?) retarded the growth of all animals, regardless of age, in 1971.

A Consideration of Three Hypotheses

Control by weather

Fuller (1967, 1969, Fuller *et al.* 1969) suggested that small mammal populations were controlled by FCP, winter, and SCP weather. Unfavorable conditions during all three periods would increase overwinter mortality and unfavorable weather during SCP would, in addition, delay spring growth, delay maturation, delay onset of breeding, decrease size of first litters, and decrease proportion of young maturing in the year of their birth. The overall effect of an unfavorable SCP, then, is to retard breeding, and hence decrease recruitment, leading to a low summer

population density.

In my study, winter mortality varied between years in the taiga and between taiga and tundra. In the taiga, overwinter mortality was important in controlling spring population density but was not related to the rate of population increase the following summer. Fuller (1969, Fuller *et al.* 1969) also concluded this from his study. On the tundra, spring population density may have been similar each year. This could have been due to either similar fall population levels and similar overwinter mortality rates or variable fall population levels and variable overwinter mortality rates. Unfortunately, my data do not allow a resolution of this problem. I suggest, however, that density independent overwinter survival may occur. Tundra microtines have been shown to select for certain types of snow conditions within the spectrum available to them (Fuller *et al.* 1975a, Pruitt 1966) and suitable overwintering habitat may be very restricted. The amount of habitat available in any winter would be dependent on amount of snowfall and winter air temperatures that year. The absolute number of successfully overwintering animals would, therefore, be set by winter conditions.

In the taiga, an unfavorable SCP delayed maturation of adults and young and delayed mean birth date of litters. However, these delays were compensated for later in the breeding season and they did not alter recruitment. No delay in spring growth, size of first litters, or proportion of young maturing was observed. An unfavorable SCP, therefore, retarded breeding to some extent but did not alter recruitment. Fuller (1969) also found no alteration in *C. rutilus* recruitment in a year with an unfavorable SCP.

My original hypothesis was that due to differences in snow cover

and environmental conditions, the effect of adverse fall, winter, and spring conditions would be more pronounced on the tundra than in the taiga and that this effect might be apparent in mortality rates, timing and intensity of reproduction, and general condition of the two populations. Although early summer tundra data were scarce, making any comparisons with taiga difficult, there appeared to be no differences in timing and intensity of reproduction or general condition between the two populations which were directly attributable to differences in environmental conditions. However, the marked difference in overwinter mortality rate between the two areas was directly related to the severity of fall, winter, and spring conditions on the tundra.

Both my study and Fuller's (1969) study offer no evidence that taiga *C. rutilus* populations are controlled by FCP, winter, and SCP weather conditions, but the tundra population I studied may have been controlled by weather conditions during these periods. This offers some support for Fuller's (1967) hypothesis.

Genetic-behavioral regulation

Chitty (1960, 1967) felt that all rodent species are capable of limiting their own population densities without destroying food resources or depending on enemies or climatic accidents. He hypothesized self-regulatory mechanisms which work through natural selection for the genotypes most fit at the various phases in a cycle. This would result in marked differences in genetic composition and behavior of populations during a cycle. Krebs (Krebs *et al.* 1973, Krebs and Myers 1974), who also felt that a single mechanism may underlie all rodent cycles, noted that the results of his studies on *Microtus* in southern Indiana, as well

as the results of studies on a number of other microtines, were consistent with Chitty's hypothesis. These cycles follow a general pattern (Krebs and Myers 1974):

> (1) Increase Phase - a period of large increase in numbers usually three-fold to six-fold over a six month period, but occasionally over 2 or even 3 years.
>
> (2) Peak Phase - a period of high numbers which may last only briefly or as much as 1 or even 2 years. In species with a well-defined peak an initial spring decline in numbers in a peak year may occur but this is followed by a more or less rapid rise in numbers so that fall numbers are similar to those in spring.
>
> (3) Decline Phase - a period of decline in numbers over a variable length of time. The decline may occur rapidly over the winter and early spring after a peak (type M), gradually over a year or less with no recovery over the breeding season (type G), or gradually over 1-2 years with some recovery during the breeding season (type H).
>
> (4) Phase of Low Numbers - a period of low numbers which is absent in some cycles and may last 1-3 years in others. Very little is known about this phase.

Considering my data in terms of a cycle, the taiga population could have been in a peak phase in 1971, in a type H decline phase in 1972, and in an increase phase in 1973; while the tundra population can only be considered to have been in a phase of low numbers all three years.

Krebs and Myers (1974) noted that certain characteristics of the population change in a cyclic manner accompanying the cycle of numbers. When the predicted trends in these biological parameters are compared with the trends observed in the taiga population (Table 26), it can be seen that the observed and expected trends coincide for only four parameters: length of breeding season, proportion of young maturing, juvenile mortality, and aggression. No data on dispersal were available from my study.

The breeding season may have been longer in 1973 (increase) than

Table 26. Comparison of trends in some biological parameters between the taiga population (observed) in 1973 (increase), 1971 (peak), and 1972 (decline) and cyclic microtines in general (expected) based on Krebs and Myers (1974).

Biological Parameter	INCREASE		PEAK		DECLINE	
	observed	expected	observed	expected	observed	expected
Reproduction						
Breeding season						
onset	average[1]	early[2]	average	intermediate	average	late
cessation	late ?	late	early	early	early	early
length	long ?	long	short	short	short	short
Age at sexual maturity	average	young	average	old	average	old ?
(proportion of young maturing)	(high)	(high)	(intermediate)	(low)	(intermediate)	(intermediate)
Mortality						
Adult mortality	average	low	average	low	average	high
Juvenile mortality	low ?	low	high	high	high	high
Growth						
Body weight	average	low	average	high	average	low
Growth rate	high ?	high	low ?	intermediate	high?	low
Aggression	low	low	high	high	low	low
Dispersal	?	high	?	intermediate	?	low

1. average = no change between phases
2. early, short, low, etc. are relative to other observed or expected phases

in the other two years but the extension is based on only one female found pregnant September II. If this animal were excluded there would have been no marked difference in the length of breeding season between years. This is not the type of extension of breeding season characteristic of cyclic microtines in an increase phase, where breeding may continue through winter.

Krebs and Myers (*Ibid.*) report cases of populations in which the proportion of young maturing in the year of their birth varied with population density. They interpreted this variation to be a change in age at sexual maturity with phase of population cycle. Although, in my study, the proportion of young breeding was higher in 1973 (increase) than in the other two years, there was no difference in age at sexual maturity. Age at sexual maturity has been inferred from body weights in many studies (*Ibid.*), but body weight is a poor measure of chronological age. Therefore age at sexual maturity is an unreliable parameter unless a good criterion for chronological age is available. I suggest that the proportion of young maturing in the year of their birth may be better related to population density (*cf.* Koshkina 1974a) than to age at sexual maturity.

In my study, early-cohort juvenile mortality did not differ between years but late-cohort mortality was probably less in 1973 (increase). This decrease did not appear to be related to weather conditions or food supply. The pattern of late-cohort juvenile mortality, therefore, fits that predicted by the cycle.

I found that wounding was generally higher in 1971 (peak) than in the other two years, which fits the pattern predicted by the cycle. However, the level of wounding has also been related to population

density directly (Christian 1971a).

Therefore, the pattern of change in some biological parameters of the taiga population over three years shows little correlation with the pattern expected for cyclic microtines in general. Krebs and Myers (1974) also noted that genetic shifts have been found between phases in cyclic microtines and that these shifts may be reflected in skull and body measurements. But variations in skull and body measurements found in my study offer no evidence of having resulted from genetic change. The tundra population I studied can be considered to have been in a phase of low numbers for three years but very little is known about this phase and no comparison between observed and expected characteristics is possible. In general, then, the populations of *C. rutilus* I studied do not offer impressive evidence of being cyclic in the sense of Krebs and Myers (*Ibid.*).

Essentially all of the microtines considered by Krebs and Myers (*Ibid.*) to be cyclic (*Microtus* spp., *Lemmus trimucronatus*, *Dicrostonyx groenlandicus*, *Clethrionomys rufocanus*) are primarily grazers (Batzli and Pitelka 1971; Hansson 1971; Koshkina 1957, 1961; Sharp 1965) and feed on a seasonal food supply; whereas *C. rutilus* and *C. gapperi* are gatherers and depend more on fruits and seeds (Dyke 1971, Koshkina 1957) which are more reliable although usually more sparsely distributed. McNab (1963) divided small mammals into those which eat fruits, seeds, and insects - hunters - and those which eat grass - croppers - and noted that, for species of about the same body weight, the home range of hunters was about four times that of croppers. He also found that home range was correlated with rate of metabolism; hunters have generally higher rates of metabolism than croppers. Therefore, he concluded,

hunters cannot generally maintain locally dense populations because of the limited amount of energy available within a given area, but croppers can, and hunters may be influenced more by environmental fluctuations than croppers.

Given these quite different life styles, it would not be surprising if populations of gatherers (hunters) were controlled/regulated in a manner quite different from grazers (croppers). Tast and Kalela (1971) observed synchronous fluctuations in four grazing microtines (*Microtus oeconomus, M. agrestis, Lemmus lemmus,* and *C. rufocanus*) but *C. rutilus* did not follow the same pattern. Krebs and Myers (1974) noted that "Some but not all species of *Clethrionomys* seem to fluctuate in regular cycles, but whether fluctuations are related to feeding habits is not clear."

Homeostatic regulation

In the Soviet Union, Koshkina studied small mammal populations in the forest and tundra of the Kola Peninsula from 1947 to 1965 (additional data were available for the period 1936-41), and in three habitat types in the Salair taiga from 1958 to 1972 (Koshkina 1957; 1965; 1966a, b; 1967a,b; 1970; and others). These observations comprise some of the longest continuous records of small mammal populations available. Populations of *C. rufocanus* and *C. glareolus* on the Kola Peninsula fluctuated and may have cycled with a 4-5 year periodicity; while *C. rutilus* populations in the Salair taiga showed variable spring population densities and remarkably similar fall densities. Based on her observations, Koshkina postulated a mechanism of population regulation for small mammals, primarily of genus *Clethrionomys* (Koshkina 1974a,b).

She felt that a homeostatic, density-dependent feedback mechanism operated to regulate population density at an optimum level, the highest level at which resources were not exhausted. The proportion of young-of-the-year which bred in the year of their birth was inversely correlated with number of overwintering animals in spring. This variable productivity compensated for variable overwinter losses and produced a high and relatively stable peak summer density. She postulated that the mechanism operated through territoriality and other social interactions. This regulatory mechanism, she noted, evolved to maintain a dynamic equilibrium between the environmental resources and animal numbers.

Homeostatic regulation, she found, operated best in species that were numerically dominant, characteristic of their habitat, and in the optimum part of their range, such as *C. rutilus* in closed forests of the Salair taiga. In associated, numerically subdominant species and in species in suboptimum habitats population regulation mechanisms were not as well-developed. Populations of *C. rufocanus* and *C. glareolus* in forest tundra of the Kola Peninsula, suboptimum habitat for these species, showed a wide variability in breeding by young, but the variability was related to migration and temporary settlement during periods of increase. The same regulatory mechanisms found in *C. rutilus* in the Salair taiga operated, but were imperfect, and did not prevent overpopulation. When regulation was unsuccessful, high population densities resulted, balance was destroyed, food was depleted, and stress appeared. This imperfect regulation resulted in high peaks followed by deep depressions.

Koshkina also observed that these homeostatic regulatory mechanisms were especially poorly developed in *L. lemmus*; increase in intensity of

breeding was observed to take place even in years of peak numbers. Rapid growth in *L. lemmus* numbers was almost unimpeded, except by emigration, and the resulting high densities depleted food supplies which could only be replenished slowly. As with populations of *C. rufocanus* and *C. glareolus*, *L. lemmus* populations experienced high peaks followed by low depressions.

These examples show variations from well-developed homeostatic regulation to its virtual absence. Koshkina noted that the method of regulation varied between species in a single area, and, within a species, between areas and between habitats in a single area. Thus, *C. rutilus* populations were observed to be best regulated in closed forest in the optimum part of their range, the Salair taiga, and to be more poorly regulated both in mixed woods and woodlots in the Salair taiga, and in forest tundra of the Kola Peninsula. In these latter areas, environmental conditions exerted more control. Koshkina noted that even when relatively well-developed, these regulatory mechanisms will sometimes fail and the balance reached will be either higher or lower than optimum, but the mechanism will eventually return the population to an optimum level.

Although one may argue with the interpretations Koshkina put on some of her data, certain conclusions central to her hypothesis are clear: (i) populations of certain species in optimum habitats, under favorable environmental conditions, are capable of regulating their densities; (ii) the mechanism operates primarily through regulating the proportion of young-of-the-year maturing in the year of their birth, and this may be accomplished through territoriality and other social interactions; (iii) in suboptimum habitats the regulatory mechanism is less well-

developed and environmental conditions may play a large role in controlling populations.

The strongest evidence Koshkina had for her hypothesis came from her work on *C. rutilus* in the Salair taiga (Koshkina 1974a). Ivanter (1974) examined small mammal populations in Karelia district, USSR, and concluded that the maintenance of optimum density and structural homeostasis in a population was secured by specific autoregulating mechanisms operating by negative feedback. He noted that the mechanism operated through varying proportion of young-of-the-year breeding and rate of sexual maturation. He also observed that this pattern was most conspicuous in *C. glareolus* and *Microtus agrestis*, the species characteristic of the habitat. In other species in the area, the effect of homeostatic mechanisms was much less and was seen only in periods of rapid increase; normally these species were controlled by extrinsic factors. Gubar' (1974) studied *C. rutilus* and *C. glareolus* populations in the Onega district of Arkhangelsk Oblast', USSR, and found density-dependent regulation of breeding in young-of-the-year but noted that the mechanisms by which it operated were unclear. He also found that poor weather inhibited summer increase in numbers.

Some populations of *Clethrionomys* in North America have also shown little variation in peak summer densities between years. Whitney (1973), working in central Alaska, found similar summer densities of *C. rutilus* over 3 years and Fuller (1974), working just west of Great Slave Lake, N.W.T., found little fluctuation in numbers of *C. rutilus* and *C. gapperi* over 4 summers. Fuller noted that densities of *C. gapperi* in early May were less than 1/ha and the maximum in August was 3/ha. He suggested that a population regulating mechanism (or mechanisms) was operating

but noted that it might have been independent of increasing population density because it was difficult to envision the necessary feedback at such low numbers.

In my study, the taiga population showed a definite relationship between spring population density and the proportion of early-cohort animals breeding, and showed similar fall population densities in 1971 and 1973. I suggest that homeostatic regulatory mechanisms, as hypothesized by Koshkina (1974a,b), were operating to attempt to maintain the population at an optimum density for the habitat. Because regulation of reproduction was not perfectly density dependent and because fall population level in 1972 was below that in the other two years, it may be that the homeostatic mechanism was operating imperfectly, as Koshkina suggested was the case for populations in suboptimal habitats. The tundra population showed no density-related regulation of reproductive rate and appeared to have been controlled by environmental conditions, findings which are also consistent with Koshkina's hypothesis.

Because my spring population densities were low, I am faced with the same question as Fuller (1974) was concerning the mechanism of feedback at low densities. Krylov (1974), working on *C. glareolus* near Moscow, USSR, found that animals lived in distinct spatial groupings in spring; the density in these groupings was about two to seven times that of the area as a whole, depending on the year and area. Social interactions within these groupings may be significant even at generally low densities. Scent communication may also play a significant role. Scent communication in most small mammals has received little attention (see Eisenberg and Kleiman 1972 and Johnson 1973 for reviews). However, subtle changes in population density may be communicated through alter-

ations in marking frequency; the frequency of scent encounters by an individual in its daily travels may be high despite a very low level of actual encounters with other individuals, especially if home ranges are large and overlapping. Both spring groupings and scent communication may function together to produce socially induced population regulation at low densities. Elliott's (1969) removal experiments on a *C. gapperi* population indicated that interaction between voles was important in determining breeding densities and territoriality has also been implicated in population regulation at both high (Bujalska 1970) and low (Smith 1973) densities. The exact role of these factors must await future study.

CONCLUSIONS

In the taiga, spring population density of *C. rutilus* declined from 1971 to 1973; while peak summer density was high in 1971 and 1973 and low in 1972. These levels were affected primarily by variations in overwintering mortality and annual production.

Population density at snowmelt was controlled by overwintering mortality rate, which varied with environmental conditions during mid-winter and spring critical period. Adverse conditions during spring critical period also delayed mean birth dates of litters but did not affect total production. An increase in productivity in 1973 was caused at least in part by a significant increase in the proportion of early-cohort females breeding. This increase appeared to have been related to low population density in early summer. A significant increase in the proportion of animals wounded was observed in 1971, the year of highest density, but there was no decrease in total production.

The taiga population appeared to have been regulated by density-dependent regulation of the proportion of early-cohort animals breeding; this seemed to have operated through feedback from spring population density. This mechanism is similar to the homeostatic, density-dependent feedback mechanism that Koshkina (1974a) postulated would regulate density at an optimum level, the highest level at which resources are not exhausted. I therefore suggest that varying overwintering mortality rates act as perturbations to the population which is then adjusted to the optimum level by this regulatory mechanism.

On the tundra, both spring and peak summer population densities were probably relatively similar between years and generally much lower than those in the taiga. The homeostatic regulatory mechanism which was found operating in the taiga population was probably also operating in the tundra population but was unable to regulate population density at the optimum level because of the extremely high overwintering mortality rate. This situation is similar to that found by Koshkina (*Ibid.*) for populations in habitats she considered to be suboptimum for the species she studied. Tundra, therefore, may be suboptimum habitat for *C. rutilus*; hence the large role played by extrinsic factors. I suggest that the tundra population is controlled by density-independent overwintering survival and that this is related to the number of suitable overwintering sites and environmental conditions during spring and fall critical periods and winter.

In conclusion, the hypotheses I set out to test have been generally rejected. Fuller's hypothesis that winter conditions can control small mammal populations (Fuller 1967, Fuller *et al.* 1969) was accepted on the tundra but rejected in the taiga, and his hypothesis that spring critical

period can control small mammal populations by advancing or retarding breeding and thus altering recruitment (Fuller 1969) was rejected in both areas.

DOMTAR
BELL-FAST BOND
50% COTTON

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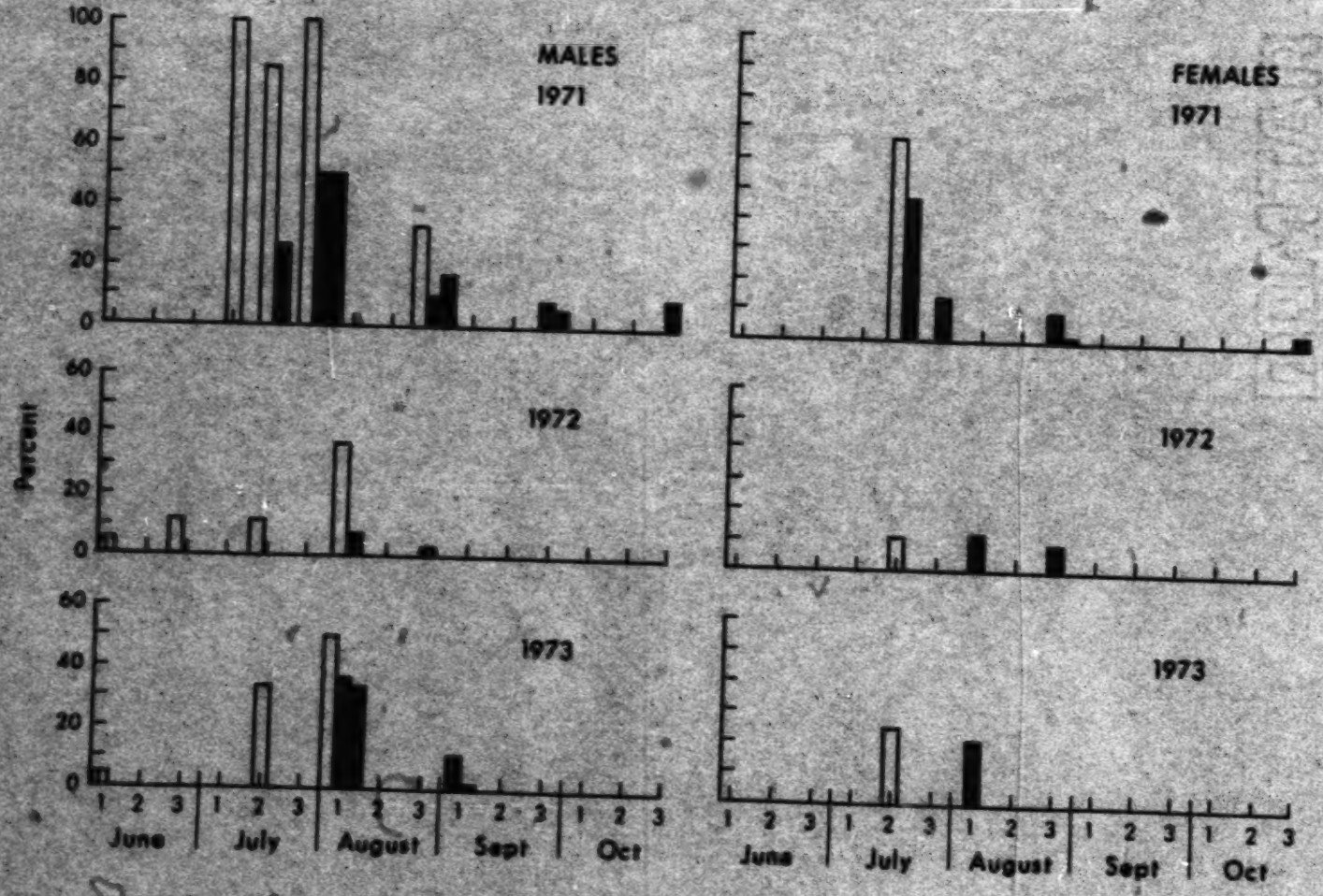
Appendix 1. Taiga population indices based on dead-trap data.

Midpoint of trapping period	Total trapnights	Total caught	Index (Number/100 trapnights) Overwintered	Early cohort	Late cohort
1971					
May 22	252	11	4.36		
June 4	888	39	4.39		
July 14	1014	63	2.66		
July 28	300	15	0.67	3.55	
Aug 28	2182	163	0.55	4.00	0.33
Sept 25	1811	140	0.56	1.28	5.65
Oct 28	600	48	0.17	1.18	5.99
				1.02	6.81
1972					
May 7	420	8	1.90		
May 27	1368	11	0.80		
June 5	3450	65	1.88		
June 25	1800	29	1.61		
July 18	3000	84	1.17	1.63	
Aug 10	3000	79	0.41	1.30	0.92
Sept 1	2460	100	0.34	0.75	2.98
Sept 24	2940	87	0.30	0.34	2.32
Oct 24	3000	42	-	0.33	1.07
1973					
May 12	600	3	0.50		
May 24	2832	28	0.99		
June 4	2670	36	1.34		
June 21	2700	24	0.82	0.07	
July 11	2400	24	0.50	0.50	
Aug 4	3300	51	0.42	0.91	0.21
Aug 22	3000	53	0.10	0.53	1.13
Sept 13	2400	164	0.21	0.67	5.92



Appendix 2. Percentage of overwintered (open), early-cohort (stippled), and late-cohort (solid) taiga animals with wounds by 10-day periods.

Appendix 3a. Paired adrenal weights (Mean ± SE) of over-wintered taiga animals April-June by 10-day periods. Sample size in parentheses.

date		male		female
Apr I	73	(8) 4.7 ± 1.21	(9)	4.9 ± 0.90
Apr II	72	(2) 3.5 ± 1.60	(3)	4.1 ± 0.61
May I	72	(4) 7.8 ± 0.99	(5)	7.0 ± 0.81
	73	(2) 7.5 ± 0.70	(1)	6.1
	71	(13) 12.2 ± 0.65	(6)	63.2 ± 7.86
May III	72	(12) 5.9 ± 0.40	(9)	9.4 ± 1.66
	73	(19) 7.5 ± 0.55	(10)	25.5 ± 5.62
	71	(38) 8.5 ± 0.49	(22)	59.4 ± 4.35
June I	72	(53) 7.2 ± 0.31	(21)	52.3 ± 4.21
	73	(20) 8.2 ± 0.64	(15)	45.5 ± 3.06
June III	72	(26) 7.8 ± 0.43	(17)	38.3 ± 3.79
	73	(12) 7.8 ± 0.84	(10)	29.6 ± 3.92

Appendix 3b. Paired adrenal weights (Mean ± SE) of taiga males July-October by 10-day periods. Sample size in parentheses.

		overwintered		early cohort breeding		early cohort non-breeding		late cohort	
July I	71	(2)	8.6 ± 0.65						
	71	(25)	6.0 ± 0.62	(1)	5.2	(16)	6.2 ± 0.61		
July II	72	(18)	7.2 ± 0.48			(26)	8.5 ± 0.40		
	73	(9)	6.2 ± 0.48			(5)	7.4 ± 0.79		
July III	71	(1)	7.9			(6)	7.5 ± 0.60		
Aug I	72	(5)	7.4 ± 0.49			(23)	7.8 ± 0.50	(18)	7.0 ± 0.51
	73	(6)	6.5 ± 0.62	(4)	12.7 ± 5.06	(7)	8.6 ± 0.81	(5)	9.3 ± 1.09
	71	(6)	5.9 ± 0.92			(19)	6.4 ± 0.56	(76)	6.4 ± 0.33
Aug III	72	(3)	6.1 ± 1.12	(1)	6.6	(8)	7.3 ± 1.48	(28)	6.4 ± 0.32
	73	(1)	7.8	(5)	10.4 ± 1.08	(3)	8.0 ± 1.44	(17)	8.4 ± 0.70
Sept II	73	(1)	9.7	(3)	7.4 ± 1.97	(5)	7.5 ± 1.23	(104)	7.1 ± 0.24
Sept III	71	(2)	5.8 ± 4.05			(12)	4.6 ± 0.37	(63)	5.0 ± 0.24
	72	(4)	7.1 ± 0.87			(5)	5.5 ± 0.44	(40)	6.0 ± 0.31
Oct III	71					(1)	5.2	(20)	4.1 ± 0.42
	72					(3)	5.2 ± 0.96	(17)	5.8 ± 0.34

Appendix 3c. Paired adrenal weights (Mean ± SE) of taiga females July-October by 10-day periods. Sample size in parentheses.

		overwintered		early cohort breeding		early cohort non-breeding		late cohort	
July I	71	(1)	77.3			(3)	44.7 ± 5.01		
July II	71	(9)	21.2 ± 2.64	(12)	37.4 ± 6.24	(14)	21.2 ± 3.28		
	72	(17)	33.1 ± 1.76			(18)	25.9 ± 5.05		
	73	(4)	25.0 ± 2.22	(2)	36.6 ± 1.05	(4)	16.1 ± 2.57		
July III	71	(1)	21.8	(2)	15.6 ± 1.35	(5)	5.9 ± 0.72		
Aug I	72	(7)	23.7 ± 3.90	(6)	25.2 ± 2.63	(12)	8.0 ± 0.79	(7)	5.8 ± 0.80
	73	(8)	19.0 ± 2.26	(16)	20.5 ± 1.62	(3)	10.9 ± 1.67	(1)	9.2
Aug III	71	(7)	21.9 ± 3.61	(6)	23.1 ± 3.89	(7)	7.1 ± 1.21	(55)	5.9 ± 0.38
	72	(6)	40.6 ± 8.23	(8)	22.0 ± 2.41	(3)	4.0 ± 0.23	(29)	5.5 ± 0.32
	73	(2)	26.6 ± 4.65	(7)	26.3 ± 2.23	(1)	11.4	(14)	9.4 ± 0.90
Sept II	73	(7)	20.2 ± 1.19	(12)	12.4 ± 1.29	(2)	5.7 ± 0.10	(82)	6.9 ± 0.31
Sept III	71	(10)	15.5 ± 1.18	(4)	9.3 ± 1.82	(7)	4.6 ± 0.63	(51)	4.9 ± 0.31
	72	(4)	16.2 ± 1.54	(5)	8.9 ± 0.76	(5)	7.2 ± 1.22	(35)	6.1 ± 0.28
Oct III	71	(1)	8.2	(4)	7.4 ± 2.39	(1)	2.8	(25)	3.9 ± 0.21
	72			(2)	8.5 ± 1.50	(5)	5.5 ± 0.60	(18)	5.7 ± 0.34

Appendix 4a. Paired kidney weights (Mean ± SE) of overwintered taiga animals April-June by 10-day periods. Sample size in parentheses.

date		male	female
Apr I	73	(8) 361 ± 16.6	(9) 354 ± 9.6
Apr II	72	(2) 267 ± 0.2	(3) 269 ± 24.5
May I	72	(4) 370 ± 17.7	(5) 336 ± 30.5
	73	(2) 356 ± 34.6	(1) 352
	71	(13) 424 ± 15.8	(6) 432 ± 9.8
May III	72	(12) 396 ± 12.1	(9) 406 ± 12.0
	73	(19) 415 ± 9.7	(10) 384 ± 9.2
	71	(37) 461 ± 8.9	(22) 399 ± 12.0
June I	72	(53) 440 ± 7.1	(21) 376 ± 6.5
	73	(20) 428 ± 8.7	(15) 370 ± 10.5
June III	72	(26) 449 ± 9.9	(17) 382 ± 12.1
	73	(12) 387 ± 13.7	(10) 361 ± 11.5

Appendix 4b. Paired kidney weights (Mean ± SE) of taiga males July-October by 10-day periods. Sample size in parentheses.

date		overwintered	early breeding	early non-breeding	late
July I	71	(2) 510 ± 61.8			
July II	71	(27) 306 ± 6.8	(1) 292	(16) 298 ± 11.6	
	72	(18) 461 ± 10.4		(26) 379 ± 10.4	
	73	(9) 345 ± 15.0		(5) 342 ± 15.8	
July III	71	(1) 380		(6) 314 ± 14.9	
Aug I	72	(5) 427 ± 20.2			
	73	(6) 365 ± 10.0	(4) 414 ± 19.0	(23) 346 ± 8.9	(18) 341 ± 9.7
				(7) 362 ± 9.6	(5) 320 ± 7.6
Aug III	71	(6) 399 ± 36.8		(19) 332 ± 10.0	(76) 366 ± 6.7
	72	(3) 477 ± 17.0	(1) 439	(8) 384 ± 21.3	(28) 366 ± 7.7
	73	(1) 351	(5) 392 ± 21.7	(3) 338 ± 20.4	(17) 364 ± 8.7
Sept II	73	(1) 354	(3) 347 ± 10.7	(5) 352 ± 12.2	(104) 366 ± 5.4
Sept III	71	(2) 341 ± 30.1		(12) 338 ± 9.5	(65) 347 ± 7.3
	72	(4) 353 ± 12.7		(5) 324 ± 11.1	(40) 350 ± 5.5
Oct III	71			(1) 316	(20) 306 ± 6.8
	72			(3) 380 ± 35.6	(17) 381 ± 9.2

Appendix 4c. Paired kidney weights (Mean ± SE) of taiga females July-October by 10-day periods. Sample size in parentheses.

		overwintered	early breeding	early non-breeding	late
July I	71	(1) 328		(3) 308 ± 48.5	
	71	(9) 283 ± 14.8	(12) 296 ± 23.6	(14) 286 ± 21.7	
July II	72	(17) 417 ± 13.4		(18) 403 ± 14.2	
	73	(4) 378 ± 22.5	(2) 360 ± 17.8	(4) 328 ± 26.1	
July III	71	(1) 236	(2) 266 ± 36.6	(5) 256 ± 4.0	
Aug I	72	(7) 344 ± 12.5	(6) 385 ± 8.2	(12) 345 ± 6.8	(7) 346 ± 20.8
	73	(8) 336 ± 14.4	(16) 336 ± 8.5	(3) 374 ± 13.8	(1) 342
	71	(7) 374 ± 14.2	(6) 350 ± 38.9	(7) 339 ± 15.5	(56) 351 ± 8.8
Aug III	72	(6) 396 ± 17.3	(8) 394 ± 18.4	(3) 388 ± 18.3	(29) 372 ± 7.7
	73	(2) 316 ± 11.4	(7) 328 ± 10.8	(1) 366	(14) 359 ± 5.9
Sept II	73	(7) 358 ± 17.6	(12) 341 ± 10.8	(2) 407 ± 3.1	(83) 370 ± 6.0
Sept III	71	(10) 317 ± 12.5	(4) 342 ± 43.6	(7) 340 ± 16.1	(51) 351 ± 7.5
	72	(14) 376 ± 13.4	(5) 347 ± 13.9	(5) 423 ± 24.9	(35) 373 ± 8.1
Oct III	71	(1) 334	(4) 304 ± 22.2	(1) 301	(25) 303 ± 4.2
	72		(2) 433 ± 7.6	(5) 385 ± 26.1	(18) 376 ± 9.3

Appendix 5a. Interscapular BAT weights (Mean ± SE) of overwintered taiga animals April-June by 10-day periods. Sample size in parentheses.

date		males		females
Apr I	73 (8)	134 ± 13.9	(9)	156 ± 12.1
Apr II	72 (2)	107 ± 10.2	(3)	131 ± 29.3
May I	72 (4)	131 ± 8.5	(5)	114 ± 10.2
	73 (2)	92 ± 10.0	(1)	80
	71 (13)	101 ± 11.3	(6)	102 ± 20.0
May III	72 (12)	70 ± 8.2	(9)	103 ± 11.4
	73 (18)	71 ± 6.9	(10)	83 ± 7.0
	71 (37)	113 ± 8.4	(19)	137 ± 13.5
June I	72 (53)	82 ± 3.8	(21)	90 ± 6.1
	73 (20)	58 ± 4.0	(15)	66 ± 6.2
June III	72 (26)	43 ± 2.6	(17)	50 ± 3.5
	73 (12)	47 ± 4.4	(10)	48 ± 5.5

Appendix 5b. Interscapular BAT weights (Mean ± SE) of taiga males July-October by 10-day periods. Sample size in parentheses.

		overwintered		early cohort breeding		early cohort non-breeding		late cohort	
July I	71	(2)	61 ± 17.8						
	71	(27)	49 ± 4.0	(1)	49	(16)	70 ± 6.5		
July II	72	(18)	40 ± 2.8			(25)	71 ± 4.9		
	73	(9)	32 ± 2.9			(5)	55 ± 15.4		
July III	71	(1)	80			(6)	114 ± 14.4		
Aug I	72	(5)	51 ± 6.0						
	73	(6)	31 ± 6.0	(4)	38 ± 2.8	(23)	62 ± 2.6	(18)	64 ± 5.1
	71	(6)	50 ± 4.2			(7)	45 ± 7.4	(5)	56 ± 8.6
Aug III	72	(3)	40 ± 3.6	(1)	61	(19)	114 ± 9.0	(76)	94 ± 3.6
	73	(1)	24	(5)	47 ± 7.9	(8)	87 ± 8.0	(28)	87 ± 4.9
						(3)	32 ± 6.6	(17)	53 ± 2.2
Sept II	73	(1)	39	(3)	50 ± 13.4	(5)	66 ± 8.1	(104)	58 ± 1.9
Sept III	71	(2)	78 ± 30.4			(12)	80 ± 9.6	(65)	89 ± 4.1
	72	(3)	57 ± 1.6			(5)	82 ± 8.6	(40)	96 ± 3.2
Oct III	71					(1)	68	(20)	100 ± 8.9
	72					(2)	60 ± 1.8	(17)	91 ± 7.0

Appendix 5c. Interscapular BAT weights (Mean ± SE) of taiga females July-October by 10-day periods. Sample size in parentheses.

		overwintered		early cohort breeding		early cohort non-breeding		late cohort	
July I	71	(1)	35			(3)	77 ± 5.1		
July II	71	(8)	48 ± 4.0	(12)	97 ± 14.6	(14)	85 ± 8.6		
	72	(16)	50 ± 5.3			(17)	76 ± 6.4		
	73	(4)	42 ± 12.4	(2)	37 ± 10.4	(4)	48 ± 11.9		
July III	71	(1)	111	(2)	71 ± 13.2	(5)	92 ± 9.6		
Aug I	72	(7)	56 ± 8.9	(5)	63 ± 11.1	(12)	79 ± 9.5	(6)	57 ± 7.8
	73	(8)	24 ± 2.8	(16)	37 ± 4.7	(3)	44 ± 14.3	(1)	23
Aug III	71	(7)	93 ± 17.1	(6)	74 ± 4.0	(7)	84 ± 8.2	(57)	107 ± 5.1
	72	(6)	59 ± 10.2	(8)	82 ± 9.4	(3)	84 ± 8.0	(27)	90 ± 5.8
	73	(2)	50 ± 0.8	(7)	31 ± 3.9	(1)	34	(14)	54 ± 4.3
Sept II	73	(7)	48 ± 3.9	(14)	48 ± 4.3	(2)	46 ± 1.3	(83)	62 ± 2.6
Sept III	71	(10)	76 ± 8.1	(4)	94 ± 24.2	(7)	79 ± 12.9	(51)	83 ± 4.7
	72	(14)	72 ± 2.6	(5)	95 ± 3.0	(5)	101 ± 7.2	(35)	94 ± 3.7
Oct III	71	(1)	96	(4)	99 ± 13.4	(1)	83	(25)	98 ± 4.9
	72			(2)	121 ± 9.4	(5)	73 ± 11.4	(18)	91 ± 6.3

Appendix 6. Paired adrenal, paired kidney, and interscapular BAT weights of taiga animals November 1971-March 1972. Sample size in parentheses.

Date	Sex		Adrenal	Kidney	BAT
Nov III	M	(7)	3.8 ± 0.39	282 ± 10.3	105 ± 8.7
	F	(14)	4.2 ± 0.32	262 ± 7.1	111 ± 8.0
Dec II	M	(10)	4.5 ± 0.42	303 ± 12.1	138 ± 11.8
	F	(5)	4.2 ± 0.96	298 ± 11.0	122 ± 13.5
Jan III	M	(13)	4.5 ± 0.40	298 ± 11.4	180 ± 11.0
	F	(12)	4.6 ± 0.56	282 ± 12.5	160 ± 15.1
March II	M	(2)	4.0 ± 0.95	318 ± 12.2	178 ± 15.0
	F	(3)	2.6 ± 0.35	307 ± 25.2	108 ± 21.9

Appendix 7a. Body lengths (Mean ± SE) of overwintered taiga animals April-June by 10-day periods. Sample size in parentheses.

	Year	Males	Females
April I	73	(8) 96.4 ± 1.15	(9) 94.9 ± 1.23
April II	72	(2) 97.5 ± 0.50	(3) 93.7 ± 0.88
May I	72	(4) 100.5 ± 1.19	(5) 95.4 ± 2.64
	73	(2) 94.5 ± 0.50	(1) 94.0
May III	71	(13) 94.8 ± 1.79	(6) 92.7 ± 1.69
	72	(12) 97.2 ± 1.54	(9) 93.7 ± 1.15
	73	(18) 97.6 ± 1.25	(10) 96.7 ± 1.28
June I	71	(38) 100.5 ± 0.90	(22) 100.8 ± 1.01
	72	(53) 100.6 ± 0.60	(21) 100.7 ± 0.81
	73	(21) 103.5 ± 1.21	(15) 102.6 ± 1.08
June III	72	(26) 106.4 ± 0.85	(18) 110.6 ± 1.34
	73	(12) 108.8 ± 0.75	(10) 109.5 ± 0.69

Appendix 7b. Body lengths (Mean ± SE) of taiga males July - October by 10-day periods. Sample size in parentheses.

	Year	overwintered	early cohort breeding	early cohort non-breeding	late cohort
July I	71	(2) 100.0 ± 7.00			
	71	(27) 104.2 ± 0.69	(1) 87.0	(16) 89.9 ± 1.10	
July II	72	(18) 107.2 ± 1.08		(26) 90.5 ± 0.83	
	73	(9) 113.6 ± 0.65		(4) 96.8 ± 1.70	
July III	71	(1) 111.0		(6) 92.8 ± 1.42	
Aug I	72	(6) 114.0 ± 1.29		(24) 101.1 ± 0.70	(19) 96.5 ± 0.80
	73	(6) 111.3 ± 2.67	(4) 101.5 ± 1.55	(7) 99.7 ± 1.48	(5) 93.6 ± 1.44
	71	(6) 102.2 ± 1.54		(19) 90.7 ± 0.93	(76) 90.7 ± 0.32
Aug III	72	(3) 109.0 ± 0.58	(1) 101.0	(8) 96.4 ± 0.86	(28) 94.4 ± 0.62
	73	(1) 107.0	(5) 101.4 ± 1.29	(3) 100.0 ± 1.00	(17) 97.5 ± 0.92
Sept II	73		(3) 105.0 ± 1.53	(5) 101.2 ± 0.37	(104) 98.2 ± 0.37
Sept III	71	(2) 105.5 ± 2.50		(12) 91.6 ± 0.76	(64) 91.2 ± 0.48
	72	(4) 112.5 ± 1.19		(5) 100.8 ± 0.58	(41) 99.6 ± 0.57
Oct III	71			(1) 92.0	(20) 93.4 ± 0.50
	72			(3) 98.0 ± 1.53	(17) 97.3 ± 0.75

Appendix 7c. Body lengths (Mean ± SE) of taiga females July - October by 10-day periods. Sample size in parentheses.

	Year	overwintered	early cohort breeding	early cohort non-breeding	late cohort
July I	71	(1) 111.0			
				(3) 89.3 ± 1.67	
July II	71	(9) 106.8 ± 3.00	(12) 97.2 ± 1.86	(14) 89.3 ± 0.85	
	72	(17) 112.1 ± 1.04		(17) 90.2 ± 0.86	
	73	(4) 115.2 ± 0.48	(2) 105.5 ± 2.50	(5) 92.8 ± 1.16	
July III	71	(1) 113.0	(2) 98.0 ± 5.00	(5) 91.4 ± 2.04	
Aug I	72	(7) 114.7 ± 1.04	(6) 109.0 ± 1.83	(12) 98.1 ± 1.02	(7) 97.3 ± 1.08
	73	(8) 115.8 ± 1.01	(16) 106.2 ± 1.14	(3) 96.7 ± 0.88	(1) 94.0
	71	(7) 108.0 ± 1.86	(6) 100.0 ± 1.29	(7) 90.4 ± 0.65	(58) 89.6 ± 0.44
Aug III	72	(6) 116.5 ± 2.08	(8) 106.4 ± 0.90	(3) 96.3 ± 1.45	(29) 92.7 ± 0.91
	73	(2) 110.0 ± 0.00	(7) 111.0 ± 2.17	(1) 103.0	(15) 96.3 ± 0.99
Sept II	73	(7) 118.9 ± 1.18	(12) 109.5 ± 0.78	(2) 97.5 ± 1.50	(83) 97.8 ± 0.36
Sept III	71	(10) 104.4 ± 1.33	(4) 103.8 ± 2.29	(7) 93.6 ± 1.29	(51) 90.6 ± 0.44
	72	(14) 118.9 ± 1.02	(5) 108.6 ± 2.73	(5) 98.4 ± 1.12	(35) 99.6 ± 0.71
Oct III	71	(1) 115.0	(4) 101.5 ± 1.32	(1) 90.0	(25) 93.7 ± 0.65
	72		(2) 107.5 ± 2.50	(5) 96.2 ± 1.16	(18) 95.4 ± 0.56

Appendix 8a. Condylobasal lengths (Mean ± SE) of overwintered taiga animals April - June by 10-day periods. Sample size in parentheses.

date		male		female	
Apr I	73	(4)	22.06 ± 0.235	(3)	21.77 ± 0.203
Apr II	72	(1)	23.55	(2)	22.58 ± 0.325
May I	72	(3)	22.75 ± 0.100	(4)	22.40 ± 0.170
	73	(2)	22.55 ± 0.000	(1)	22.40
	71	(12)	23.21 ± 0.197	(6)	22.83 ± 0.242
May III	72	(5)	23.25 ± 0.182	(8)	22.41 ± 0.181
	73	(11)	22.97 ± 0.172	(8)	22.41 ± 0.181
	71	(30)	23.36 ± 0.092	(15)	22.94 ± 0.126
June I	72	(27)	23.40 ± 0.093	(10)	23.32 ± 0.121
	73	(13)	23.29 ± 0.141	(6)	23.22 ± 0.242
June III	72	(16)	23.66 ± 0.126	(17)	23.97 ± 0.121
	73	(7)	23.66 ± 0.236	(5)	23.58 ± 0.262

Appendix 8b. Condylobasal lengths (Mean ± SE) of taiga males July-October by 10-day periods. Sample size in parentheses.

	overwintered		early breeding		early non-breeding		late	
July I	71	(2) 24.02 ± 0.175						
	71	(23) 23.53 ± 0.125			(12)	21.40 ± 0.233		
July II	72	(11) 24.02 ± 0.202			(11)	21.11 ± 0.169		
	73	(3) 24.28 ± 0.196			(4)	21.68 ± 0.250		
July III	71				(5)	22.14 ± 0.200		
Aug I	72	(2) 24.35 ± 0.750			(14)	22.64 ± 0.108	(13)	21.95 ± 0.104
	73	(2) 23.55 ± 0.350	(1)	23.00	(3)	22.68 ± 0.044	(4)	21.81 ± 0.322
	71	(6) 23.42 ± 0.116			(13)	22.60 ± 0.134	(59)	22.13 ± 0.805
Aug III	72	(1) 23.45	(1)	23.10	(5)	22.42 ± 0.174	(18)	21.86 ± 0.095
	73	(1) 23.75	(4)	22.88 ± 0.157	(2)	22.68 ± 0.375	(11)	21.60 ± 0.207
Sept II	73		(1)	22.50	(4)	22.72 ± 0.284	(67)	22.37 ± 0.094
Sept III	71				(12)	22.30 ± 0.769	(43)	22.07 ± 0.107
	72	(2) 24.25 ± 0.050			(4)	22.85 ± 0.241	(23)	22.31 ± 0.171
Oct III	71						(17)	22.12 ± 0.934
	72						(12)	22.27 ± 0.111

Appendix 8c. Condylobasal lengths (Mean ± SE) of taiga females July - October by 10-day periods. Sample size in parentheses.

	overwintered		early breeding		early non-breeding		late	
July I	71	(1) 22.55						
					(3)	21.88 ± 0.300		
	71	(6) 23.96 ± 0.258	(10)	22.30 ± 0.239	(9)	21.30 ± 0.179		
July II	72	(11) 24.12 ± 0.090			(11)	21.53 ± 0.197		
	73	(1) 23.40	(1)	22.65	(3)	21.65 ± 0.229		
July III	71	(1) 24.25						
					(4)	21.45 ± 0.237		
Aug I	72	(3) 24.32 ± 0.296	(6)	23.20 ± 0.290	(8)	22.44 ± 0.142	(6)	21.95 ± 0.093
	73	(6) 24.51 ± 0.139	(10)	23.08 ± 0.119	(2)	21.75 ± 0.250	(1)	21.50
	71	(7) 23.78 ± 0.231	(6)	22.92 ± 0.229	(6)	22.53 ± 0.138	(41)	21.71 ± 0.123
Aug III	72	(5) 24.53 ± 0.206	(6)	23.18 ± 0.054	(2)	22.58 ± 0.575	(19)	21.40 ± 0.128
	73	(2) 23.35 ± 0.400	(3)	23.53 ± 0.245	(1)	22.75	(7)	21.82 ± 0.282
Sept II	73	(1) 23.65	(6)	22.98 ± 0.208	(1)	22.85	(53)	22.18 ± 0.115
Sept III	71	(5) 23.78 ± 0.165	(3)	23.77 ± 0.368	(6)	22.36 ± 0.070	(35)	22.06 ± 0.096
	72	(8) 24.54 ± 0.287	(3)	23.85 ± 0.076	(4)	22.15 ± 0.352	(18)	22.47 ± 0.164
Oct III	71	(1) 24.45	(2)	22.32 ± 0.025	(1)	21.85	(17)	22.29 ± 0.921
	72		(2)	22.88 ± 0.075	(4)	22.08 ± 0.293	(12)	21.96 ± 0.124

Appendix 9a. Corrected body weights (Mean ± SE) of overwintered taiga animals April - June by 10-day periods. Sample size in parentheses.

		Year	males		females	
April	I	73	(8)	15.2 ± 0.50	(9)	14.7 ± 0.46
April	II	72	(2)	16.6 ± 0.99	(3)	15.4 ± 0.39
May	I	72	(4)	19.1 ± 0.52	(5)	18.4 ± 0.71
		73	(2)	19.5 ± 1.17	(1)	18.1
		71	(13)	21.0 ± 0.55	(6)	17.2 ± 0.70
May	III	72	(12)	20.3 ± 0.53	(9)	16.6 ± 0.43
		73	(19)	20.3 ± 0.65	(10)	17.3 ± 0.63
		71	(38)	23.2 ± 0.44	(22)	22.0 ± 0.63
June	I	72	(55)	22.1 ± 0.24	(21)	20.3 ± 0.42
		73	(21)	23.1 ± 0.47	(15)	21.9 ± 0.63
June	III	72	(26)	24.6 ± 0.39	(17)	25.6 ± 0.70
		73	(12)	24.7 ± 0.46	(10)	24.4 ± 0.46

Appendix 9b. Corrected body weights (Mean ± SE) of taiga males July - October by 10-day periods. Sample size in parentheses.

	Year	overwintered	early cohort breeding	early cohort non-breeding	late cohort
July I	71	(2) 24.4 ± 1.66			
July II	71	(27) 26.6 ± 0.46	(1) 15.2	(16) 15.2 ± 0.40	
	72	(18) 26.3 ± 0.52		(26) 14.2 ± 0.39	
	73	(9) 27.3 ± 1.22		(5) 17.0 ± 0.62	
July III	71	(1) 27.8		(6) 16.8 ± 0.44	
Aug I	72	(5) 26.3 ± 0.52		(24) 16.7 ± 0.25	(18) 15.7 ± 0.29
	73	(6) 27.9 ± 0.96	(4) 20.0 ± 0.91	(7) 17.4 ± 0.22	(5) 16.8 ± 0.90
Aug III	71	(6) 26.1 ± 1.48		(19) 17.7 ± 0.36	(76) 17.2 ± 0.17
	72	(5) 25.6 ± 1.07	(1) 19.6	(8) 16.1 ± 0.37	(28) 15.6 ± 0.28
	73	(1) 25.8	(5) 20.0 ± 1.35	(3) 16.9 ± 0.74	(17) 15.2 ± 0.62
Sept II	73	(1) 25.8	(3) 21.0 ± 0.46	(5) 18.4 ± 0.48	(104) 17.0 ± 0.17
Sept III	71	(2) 22.7 ± 0.34		(12) 18.8 ± 0.20	(65) 18.1 ± 0.24
	72	(4) 26.8 ± 0.85		(5) 19.2 ± 0.54	(40) 18.6 ± 0.34
Oct III	71			(1) 15.5	(20) 16.6 ± 0.22
	72			(3) 15.9 ± 1.26	(17) 16.1 ± 0.17

Appendix 9c. Corrected body weights (Mean ± SE) of taiga females July - October by 10-day periods. Sample size in parentheses.

	Year	overwintered	early cohort breeding	early cohort non-breeding	late cohort
July I	71	(1) 27.9		(3) 17.0 ± 0.55	
July II	71	(9) 27.3 ± 1.20	(12) 19.6 ± 1.05	(14) 15.8 ± 0.50	
	72	(17) 27.8 ± 0.47		(18) 14.8 ± 0.55	
	73	(4) 25.0 ± 1.29	(2) 19.9 ± 1.35	(4) 14.1 ± 1.33	
July III	71	(1) 33.1	(2) 22.8 ± 0.29	(5) 16.9 ± 0.26	
Aug I	72	(7) 27.3 ± 0.91	(6) 22.1 ± 1.57	(12) 16.3 ± 0.36	(7) 15.6 ± 0.73
	73	(8) 26.1 ± 1.23	(16) 24.9 ± 0.61	(3) 16.8 ± 0.74	(1) 16.3
Aug III	71	(7) 26.9 ± 1.54	(6) 23.7 ± 1.45	(7) 17.4 ± 0.61	(57) 16.5 ± 0.28
	72	(6) 27.2 ± 0.86	(8) 20.8 ± 0.60	(3) 15.9 ± 0.44	(29) 14.7 ± 0.30
	73	(2) 28.4 ± 0.14	(7) 27.4 ± 1.19	(1) 16.7	(15) 15.3 ± 0.60
Sept II	73	(7) 29.0 ± 1.81	(12) 24.2 ± 0.77	(2) 16.6 ± 1.02	(82) 16.6 ± 0.17
Sept III	71	(10) 24.5 ± 0.88	(4) 22.5 ± 0.55	(7) 18.7 ± 0.72	(51) 17.8 ± 0.22
	72	(14) 27.7 ± 0.60	(5) 23.5 ± 0.64	(5) 18.1 ± 0.83	(35) 18.0 ± 0.34
Oct III	71	(1) 24.2	(4) 19.2 ± 0.56	(1) 14.3	(25) 16.6 ± 0.21
	72		(2) 18.1 ± 0.87	(5) 15.3 ± 0.51	(18) 15.0 ± 0.30

Appendix 10. Statistical differences (by t-test) in mean body length, condylobasal length, and corrected body weight between taiga males and females.

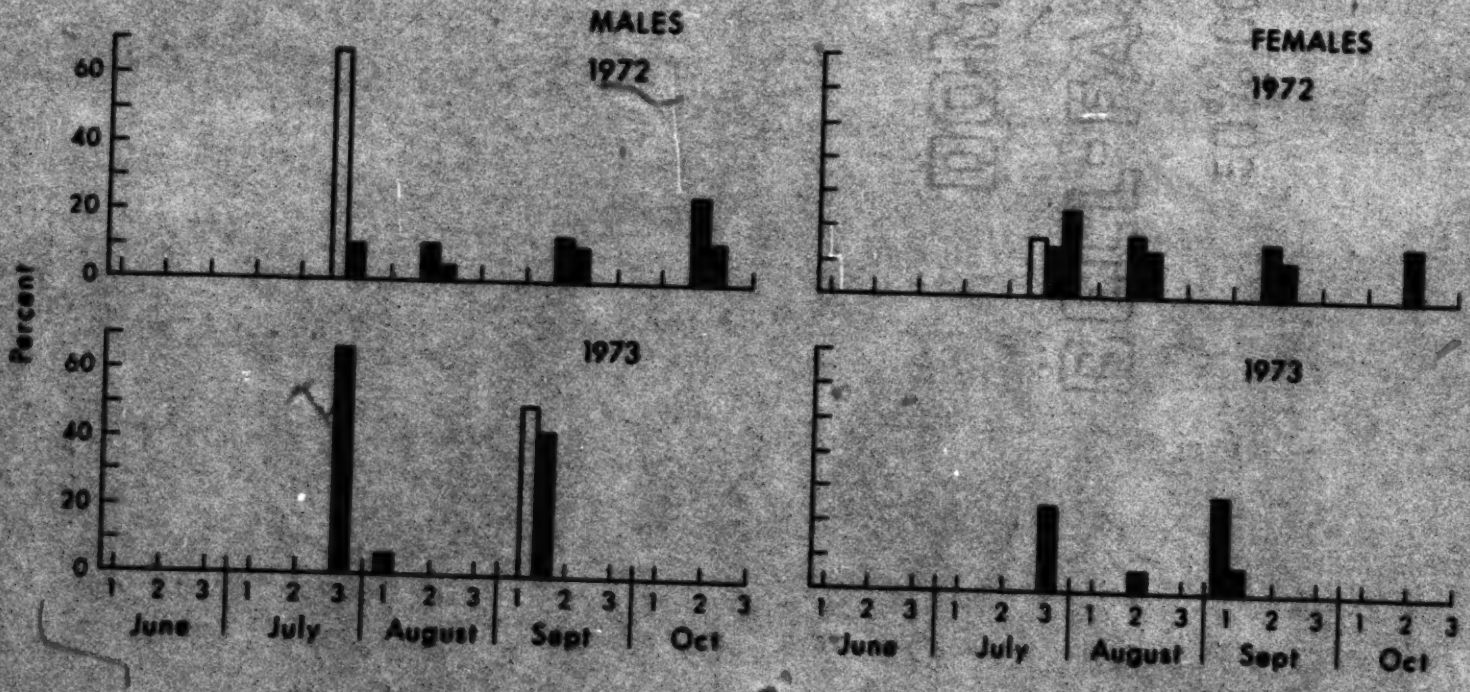
Sampling period		overwintered			early cohort non-breeding			late cohort		
		71	72	73	71	72	73	71	72	73
Body length										
Apr	I			-						
	II		*							
May	I		-	-						
	III	-	-	-						
June	I	-	-	-						
	III		**	-						
July	I	-								
	II	-	*	-	-	-	-			
	III	0			-					
Aug	I		-	-		*	-		-	-
	III	*	*	0	-	-	-	*	-	-
Sept	II						*			-
	III	-	**		-	-				
Oct	III				0	-		-	*	
Condylobasal length										
Apr	I			-						
	II		-							
May	I		-	-						
	III	-	*	*						
June	I	*	-	-						
	III		-	-						
July	I	*								
	II	-	-	-	-	-	-			
	III				-					
Aug	I		-	*		-	**			
	III	-	-	-	-	-	-	**	**	-
Sept	II						-			-
	III		-		-	-		-	-	
Oct	III							-	-	
Corrected body weight										
Apr	I			-						
	II		-							
May	I		-	-						
	III	***	***	**						
June	I	-	***	-						
	III		-	-						
July	I	-								
	II	-	*	-	-	-	-			
	III	0			-					
Aug	I		-	-		-	-		-	-
	III	*	-	-	-	-	-	*	*	-
Sept	II			-			-			-
	III	-	-		-	-		-	-	
Oct	III				0	-		-	**	

0 = could not be tested
- = not significant, $p > 0.05$
* = $0.05 > p > 0.01$
** = $0.01 > p > 0.001$
*** = $p < 0.001$

Appendix 11. Tundra population indices, based on dead-trap data.

Midpoint of trapping period	Site*	Total trapnights	Total caught	Index (Number/100 trapnights) Overwintered	Early cohort	Late cohort
1971						
June 16	T	300	4	1.33		
June 29	1,1a	700	2	0.28		
July 21	T	600	6	0.28	0.71	
Aug 14	1,1a	690	10	0.14	1.01	0.29
1972						
June 19	1	2550	6	0.24		
July 5	2	4800	30	0.45	0.16	
July 31	3	6000	75	0.15	1.01	0.08
Aug 20	4	5400	121	0.11	1.19	0.94
Sept 14	5	3000	196	0.38	1.62	4.54
Oct 14	5	2100	82	0.15	0.78	2.97
1973						
June 12	1	3000	0	0.00		
July 4	2	6000	35	0.20	0.38	
July 28	3	3000	12	0.03	0.33	0.03
Aug 14	4	3000	25	0.03	0.30	0.50
Sept 1	5	2964	63	0.13	0.51	1.48

* 1-5 = primary study sites (Fig. 1)
T = Tuktoyaktuk study site



Appendix 12. Percentage of overwintered (open), early-cohort (stippled), and late-cohort (solid) tundra animals with wounds by 10-day periods.

Appendix 13a. Paired adrenal weights (Mean ± SE) of tundra males June - October by 10-day periods. Sample size in parentheses.

		overwintered	early breeding	early non-breeding	late
		(n) mean ± SE	(n) mean ± SE	(n) mean ± SE	(n) mean ± SE
June II	71	(2) 7.3 ± 1.50			
	72	(2) 4.4 ± 0.35			
July I	72	(6) 8.3 ± 0.72			
	73	(5) 8.6 ± 0.41		(2) 3.3 ± 0.80	
				(8) 5.8 ± 0.81	
July III	71	(1) 6.8			
	72	(3) 7.3 ± 1.52	(2) 7.4 ± 2.10		
	73		(12) 6.4 ± 0.47	(19) 6.3 ± 0.59	
			(5) 7.8 ± 1.07	(1) 10.9	
Aug II	71	(1) 5.3			
	72	(5) 6.9 ± 0.85	(6) 4.7 ± 0.73		(2) 8.6 ± 0.16
	73		(2) 5.3 ± 1.00	(29) 6.8 ± 0.38	(22) 6.7 ± 0.36
			(1) 3.6	(12) 6.3 ± 0.55	(32) 6.5 ± 0.49
Sept I	73	(2) 5.8 ± 1.15	(2) 6.6 ± 1.15	(12) 6.4 ± 0.64	(20) 6.9 ± 0.39
Sept II	72	(2) 5.6 ± 0.95		(24) 5.6 ± 0.44	(75) 5.3 ± 0.16
Oct II	72	(1) 5.2		(12) 5.5 ± 0.54	(31) 5.2 ± 0.23

Appendix 13b. Paired adrenal weights (Mean ± SE) of tundra females June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	42.8 ± 4.35						
	72	(4)	41.8 ± 6.49						
June III	71	(2)	26.6 ± 2.65						
July I	72	(16)	33.7 ± 0.26						
	73	(7)	34.0 ± 2.84			(6)	38.6 ± 7.65		
	71	(1)	25.6	(5)	35.0 ± 2.88				
July III	72	(6)	32.2 ± 4.36	(17)	36.0 ± 2.75	(9)	16.1 ± 8.91		
	73	(1)	21.5	(2)	16.2 ± 3.70	(2)	10.2 ± 2.15		
	71			(2)	20.8 ± 0.65			(1)	6.4
Aug II	72	(1)	28.6	(23)	22.6 ± 1.36	(10)	7.7 ± 0.50	(18)	5.6 ± 0.40
	73	(2)	23.0 ± 2.55	(5)	16.2 ± 2.29	(5)	6.6 ± 0.74	(26)	6.0 ± 0.33
Sept I	73	(3)	20.9 ± 1.32	(7)	13.2 ± 0.97	(7)	5.9 ± 0.84	(41)	5.9 ± 0.30
Sept II	72	(10)	19.9 ± 1.51	(9)	12.0 ± 1.89	(17)	5.0 ± 0.36	(67)	5.4 ± 0.19
Oct II	72	(2)	9.2 ± 0.90	(4)	7.0 ± 0.32			(24)	5.4 ± 0.40

Appendix 14a. Paired kidney weights (Mean ± SE) of tundra males June - October by 10-day periods. Sample size in parentheses.

		overwintered (n) mean ± SE	early breeding (n) mean ± SE	early non-breeding (n) mean ± SE	late (n) mean ± SE
June II	71	(2) 406 ± 13.5			
	72	(2) 446 ± 11.6			
July I	72	(6) 498 ± 14.6		(2) 421 ± 18.2	
	73	(5) 376 ± 30.9		(8) 312 ± 16.2	
	71	(1) 446	(2) 424 ± 8.4		
July III	72	(3) 492 ± 10.5	(19) 437 ± 18.2	(13) 520 ± 15.2	
	73		(5) 449 ± 13.5	(1) 339	
	71	(1) 418	(6) 413 ± 23.6		(2) 432 ± 0.8
Aug II	72	(5) 439 ± 22.1	(2) 391 ± 88.0	(28) 461 ± 11.8	(22) 432 ± 14.3
	73	(1) 521	(1) 372	(12) 374 ± 11.0	(32) 345 ± 8.2
Sept I	73	(2) 377 ± 33.6	(2) 408 ± 32.6	(12) 384 ± 15.4	(20) 352 ± 9.3
Sept II	72	(2) 361 ± 31.3		(24) 380 ± 7.5	(75) 375 ± 5.3
Oct II	72	(1) 298		(12) 333 ± 11.3	(31) 351 ± 8.8

Appendix 14b. Paired kidney weights (Mean ± SE) of tundra females June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	331 ± 10.1						
	72	(4)	401 ± 20.2						
June III	71	(2)	339 ± 26.2						
July I	72	(16)	403 ± 13.6						
	73	(7)	308 ± 6.8			(6)	346 ± 25.8		
July III	71	(1)	334	(3)	386 ± 33.2				
	72	(6)	395 ± 11.4	(9)	412 ± 17.1	(17)	430 ± 18.6		
	73	(1)	362	(2)	320 ± 15.0	(2)	439 ± 38.0		
Aug II	71			(2)	330 ± 7.7			(1)	472
	72	(1)	411	(23)	392 ± 10.6	(10)	464 ± 26.2	(18)	419 ± 8.8
	73	(2)	312 ± 26.0	(5)	310 ± 12.8	(5)	435 ± 28.7	(26)	354 ± 9.5
Sept I	73	(3)	352 ± 43.3	(7)	369 ± 18.3	(7)	410 ± 14.2	(41)	371 ± 5.0
Sept II	72	(10)	368 ± 8.0	(9)	382 ± 13.2	(17)	364 ± 10.5	(67)	372 ± 4.5
Oct II	72	(2)	400 ± 34.5	(4)	390 ± 10.1			(24)	348 ± 8.2

Appendix 15a. Interscapular BAT weights (Mean ± SE) of tundra males June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	118 ± 27.0						
	72	(2)	71 ± 3.8						
July I	72	(6)	53 ± 7.8			(2)	86 ± 14.3		
	73	(5)	59 ± 4.2			(8)	84 ± 10.9		
	71	(1)	94	(2)	80 ± 1.4				
July III	72	(3)	49 ± 7.8	(13)	54 ± 3.9	(19)	68 ± 5.7		
	73			(5)	50 ± 11.9	(1)	26		
	71			(6)	90 ± 10.8			(2)	148 ± 40.5
Aug II	72	(4)	54 ± 8.3	(2)	52 ± 0.7	(29)	61 ± 4.8	(22)	75 ± 5.0
	73	(1)	44	(1)	65	(12)	55 ± 5.8	(31)	59 ± 3.1
Sept I	73	(2)	47 ± 6.8	(2)	55 ± 16.7	(12)	51 ± 5.8	(19)	49 ± 4.4
Sept II	72	(2)	52 ± 15.0			(15)	80 ± 4.3	(75)	87 ± 2.6
Oct II	72	(1)	61			(11)	84 ± 6.4	(29)	86 ± 4.3

Appendix 15b. Interscapular BAT weights (Mean ± SE) of tundra females June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	98 ± 40.2						
	72	(4)	87 ± 14.8						
June III	71	(2)	66 ± 14.8						
July I	72	(16)	55 ± 4.0						
	73	(7)	60 ± 6.8			(6)	74 ± 21.1		
	71	(1)	81	(3)	119 ± 27.9				
July III	72	(6)	55 ± 3.8	(17)	59 ± 4.7	(9)	84 ± 8.6		
	73	(1)	24	(2)	90 ± 27.6	(2)	64 ± 32.8		
	71			(2)	35 ± 13.0			(1)	63
Aug II	72	(1)	43	(23)	48 ± 4.5	(10)	69 ± 6.7	(18)	86 ± 9.0
	73	(2)	38 ± 1.3	(5)	35 ± 2.9	(5)	50 ± 5.5	(25)	60 ± 3.6
Sept I	73	(3)	44 ± 12.3	(7)	33 ± 4.6	(7)	43 ± 6.9	(40)	57 ± 3.9
Sept II	72	(10)	61 ± 8.6	(9)	72 ± 6.0	(17)	83 ± 4.4	(67)	86 ± 2.9
Oct II	72	(2)	74 ± 12.4	(4)	92 ± 13.8			(23)	81 ± 5.9

Appendix 16a. Body lengths (Mean ± SE) of tundra males June - October by 10-day periods. Sample size in parentheses.

		overwintered (n) mean ± SE	early breeding (n) mean ± SE	early non-breeding (n) mean ± SE	late (n) mean ± SE
June II	71	(2) 96.5 ± 0.50			
	72	(2) 104.5 ± 0.50			
July I	72	(6) 105.7 ± 1.12			
	73	(5) 110.2 ± 1.59		(2) 93.5 ± 3.50	
				(8) 91.8 ± 1.67	
	71	(1) 104	(2) 95.0 ± 2.00		
July III	72	(3) 106.7 ± 1.20	(13) 96.7 ± 1.49	(18) 92.5 ± 1.04	
	73		(5) 103.6 ± 1.33	(1) 100	
	71	(1) 99	(6) 95.0 ± 2.16		(2) 92.0 ± 0.00
Aug II	72	(5) 105.0 ± 1.10	(2) 93.5 ± 5.50	(29) 94.9 ± 0.88	(22) 93.9 ± 0.65
	73	(1) 111	(1) 105	(12) 101.4 ± 0.77	(32) 97.1 ± 0.84
Sept I	73	(2) 110.5 ± 0.50	(2) 105.0 ± 0.00	(12) 102.6 ± 0.84	(20) 98.6 ± 0.77
Sept II	72	(2) 118.5 ± 1.50		(24) 101.2 ± 0.74	(75) 99.5 ± 0.40
Oct II	72	(1) 102		(12) 99.3 ± 1.31	(33) 97.2 ± 0.98

Appendix 16b. Body lengths (Mean ± SE) of tundra females June - October by 10-day periods. Sample size in parentheses.

		overwintered	early breeding	early non-breeding	late
		(n) mean ± SE	(n) mean ± SE	(n) mean ± SE	(n) mean ± SE
June II	71	(2) 103.0 ± 4.00			
	72	(4) 105.5 ± 2.53			
June III	71	(2) 107.5 ± 2.50			
July I	72	(16) 108.7 ± 1.25			
	73	(7) 116.0 ± 1.45			
				(6) 93.7 ± 1.45	
	71	(1) 110	(3) 97.0 ± 1.00		
July III	72	(6) 110.0 ± 1.03	(16) 100.9 ± 0.86	(11) 89.2 ± 1.70	
	73	(1) 120	(2) 111.0 ± 1.00	(2) 99.5 ± 2.50	
	71		(2) 101.5 ± 3.50		
Aug II	72	(1) 111	(23) 102.9 ± 0.92	(10) 95.6 ± 1.02	(1) 91
	73	(2) 119.0 ± 1.00	(5) 113.0 ± 0.84	(5) 100.4 ± 1.29	(18) 91.9 ± 0.88
					(26) 97.4 ± 0.84
Sept I	73	(3) 124.3 ± 0.88	(7) 109.6 ± 1.77	(7) 100.8 ± 0.91	(41) 99.0 ± 0.64
Sept II	72	(10) 122.7 ± 0.92	(9) 108.9 ± 1.49	(17) 101.1 ± 0.52	(66) 99.2 ± 0.49
Oct II	72	(2) 121.0 ± 1.00	(4) 107.2 ± 4.77		(26) 95.6 ± 0.86

Appendix 17a. Condylobasal lengths (Mean ± SE) of tundra males June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	23.02 ± 0.225						
	72	(2)	22.82 ± 0.750						
July I	72	(4)	23.44 ± 0.418						
	73	(4)	23.62 ± 0.263			(1)	21.65		
						(4)	20.94 ± 0.168		
July III	71			(1)	21.55				
	72	(2)	24.15 ± 0.250	(12)	22.45 ± 0.146	(16)	21.85 ± 0.183		
	73			(4)	22.70 ± 0.087	(1)	22.05		
Aug II	71	(1)	23.00	(5)	22.54 ± 0.165			(2)	22.18 ± 0.025
	72	(3)	23.85 ± 0.200			(22)	22.60 ± 0.098	(10)	21.67 ± 0.258
	73	(1)	24.05	(1)	22.90	(7)	22.76 ± 0.218	(21)	21.80 ± 0.186
Sept I	73	(1)	23.60	(2)	22.98 ± 0.025	(9)	23.04 ± 0.179	(13)	22.11 ± 0.221
Sept II	72	(1)	24.65			(16)	22.81 ± 0.109	(51)	22.52 ± 0.094
Oct II	72	(1)	25.45			(10)	22.78 ± 0.097	(21)	22.56 ± 0.135

Appendix 17b. Condylobasal lengths (Mean ± SE) of tundra females June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	23.05 ± 0.050						
	72	(2)	22.90 ± 0.050						
June III	71	(1)	23.55						
July I	72	(11)	23.43 ± 0.174						
	73	(5)	23.73 ± 0.168			(3)	20.72 ± 0.344		
	71			(3)	22.25 ± 0.189				
July III	72	(4)	23.55 ± 0.151	(11)	22.60 ± 0.223	(8)	20.85 ± 0.239		
	73					(2)	22.38 ± 0.125		
	71			(2)	22.28 ± 0.025				
Aug II	72	(1)	24.60	(15)	22.99 ± 0.138	(6)	22.45 ± 0.239	(4)	21.24 ± 0.546
	73	(1)	24.30	(4)	23.68 ± 0.198	(5)	22.46 ± 0.143	(17)	21.51 ± 0.148
Sept I	73	(1)	24.40	(1)	23.25	(4)	23.12 ± 0.249	(20)	22.04 ± 0.195
Sept II	72	(7)	24.69 ± 0.141	(7)	23.59 ± 0.109	(11)	22.74 ± 0.123	(33)	22.36 ± 0.118
Oct II	72	(1)	24.15	(3)	23.43 ± 0.235			(21)	22.40 ± 0.114

Appendix 18a. Corrected body weights (Mean ± SE) of tundra males June - October by 10-day periods. Sample size in parentheses.

		overwintered		early breeding		early non-breeding		late	
		(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE	(n)	mean ± SE
June II	71	(2)	23.3 ± 0.70						
	72	(2)	21.3 ± 1.61						
July I	72	(6)	26.3 ± 1.09			(2)	14.1 ± 1.76		
	73	(5)	24.0 ± 0.73			(8)	15.1 ± 0.49		
	71	(1)	23.4	(2)	17.8 ± 0.95				
July III	72	(3)	26.0 ± 0.62	(13)	18.2 ± 0.48	(19)	15.8 ± 0.35		
	73			(5)	19.3 ± 0.42	(1)	16.5		
	71	(1)	28.4	(6)	21.0 ± 0.80			(2)	17.9 ± 0.30
Aug II	72	(5)	25.9 ± 0.63	(2)	20.0 ± 1.08	(29)	17.6 ± 0.23	(32)	15.4 ± 0.42
	73	(1)	20.0	(1)	22.2	(12)	18.6 ± 0.31	(32)	16.0 ± 0.40
Sept I	73	(2)	25.5 ± 0.15	(2)	22.0 ± 1.44	(12)	19.0 ± 0.39	(20)	17.3 ± 0.43
Sept II	72	(2)	28.0 ± 0.46			(24)	20.1 ± 0.29	(75)	18.5 ± 0.22
Oct II	72	(1)	26.7			(12)	18.0 ± 0.23	(31)	17.8 ± 0.25

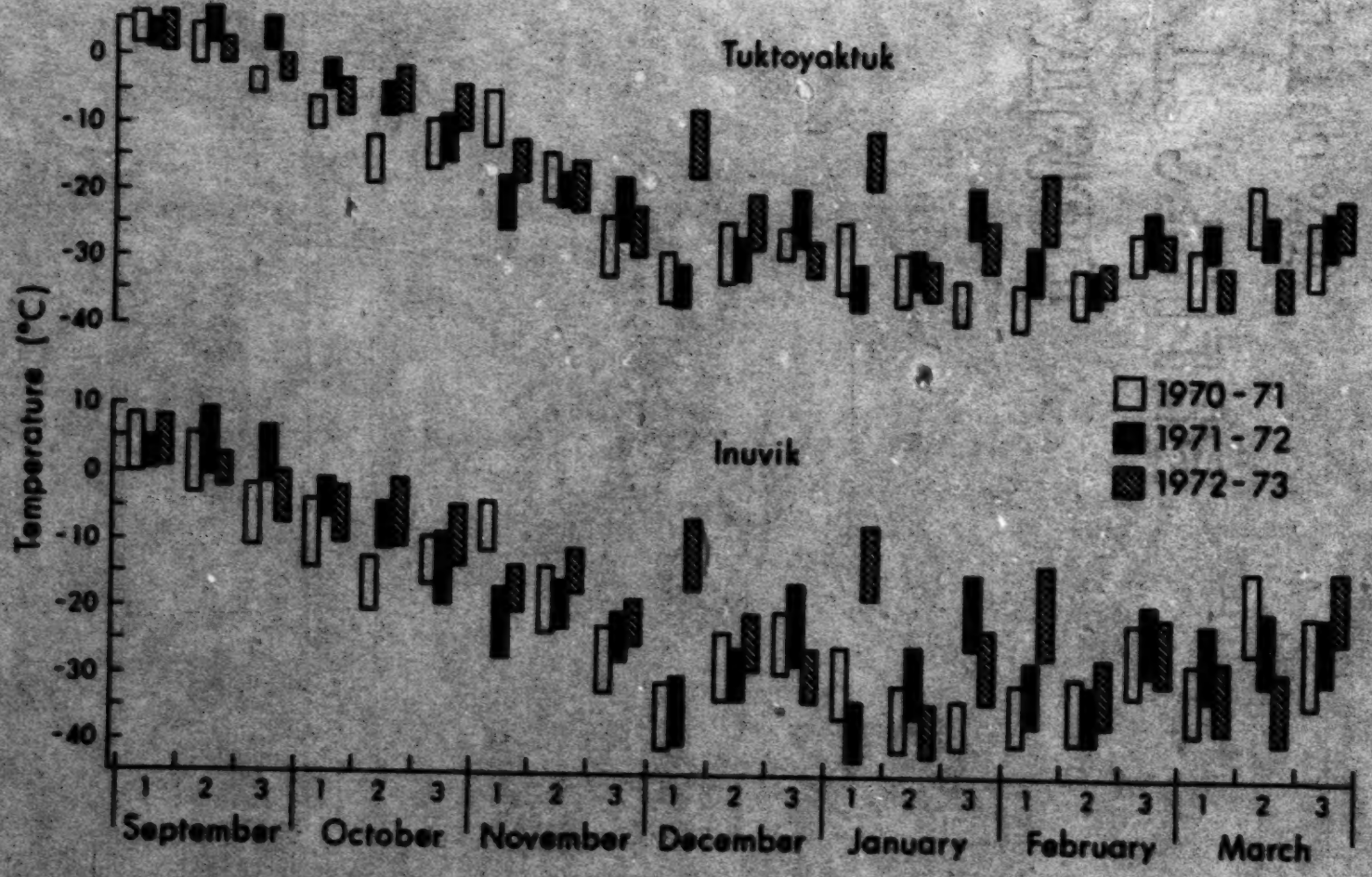
Appendix 18b. Corrected body weights (Mean ± SE) of tundra females June - October by 10-day periods. Sample size in parentheses.

		overwintered (n) mean ± SE	early breeding (n) mean ± SE	early non-breeding (n) mean ± SE	late (n) mean ± SE
June II	71	(2) 22.2 ± 1.95			
	72	(4) 21.1 ± 1.15			
June III	71	(2) 25.4 ± 0.30			
July I	72	(16) 25.4 ± 0.66			
	73	(7) 25.8 ± 0.51			
				(6) 14.1 ± 1.11	
	71	(1) 26.9	(3) 19.7 ± 0.81		
July III	72	(6) 27.4 ± 1.02	(17) 21.7 ± 0.65	(9) 13.7 ± 0.71	
	73	(1) 27.4	(2) 24.6 ± 0.08	(2) 13.6 ± 0.06	
	71		(2) 26.4 ± 0.81		(1) 14.2
Aug II	72	(1) 26.3	(23) 24.0 ± 0.59	(10) 16.9 ± 0.21	(17) 15.5 ± 0.39
	73	(2) 30.0 ± 0.70	(5) 27.9 ± 1.43	(5) 17.8 ± 0.16	(26) 16.0 ± 0.40
Sept I	73	(3) 33.4 ± 3.83	(7) 25.3 ± 1.27	(7) 18.6 ± 0.49	(41) 17.0 ± 0.33
Sept II	72	(10) 29.9 ± 0.84	(9) 24.3 ± 0.36	(17) 19.8 ± 0.30	(67) 17.7 ± 0.27
Oct II	72	(2) 25.1 ± 0.31	(4) 21.7 ± 1.70		(24) 17.5 ± 0.30

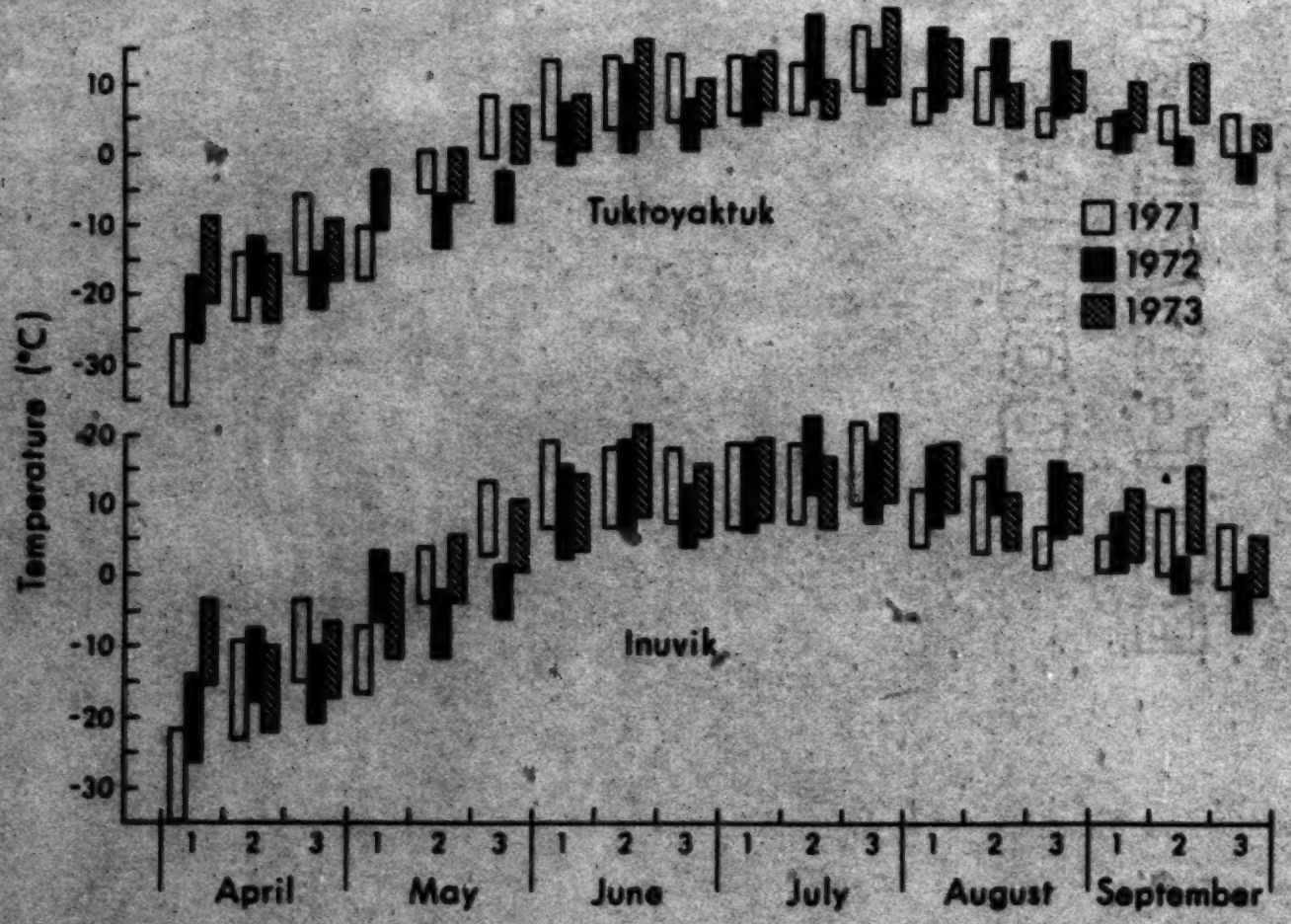
Appendix 19. Statistical differences (by t-test) in mean body length, condylobasal length, and corrected body weight between tundra males and female

Sampling period		Overwintered 71	72	73	Early cohort 71	72	73	Late cohort 71	72	73
Body length										
June	II	-	-							
	III									
July	I		-	*			-			
	III	0	-			-	-			
Aug	II		-	-		-	-	0	-	-
Sept	I			***			-			-
	II		-			-			-	
Oct	II		-						-	
Condylobasal length										
June	II	-	-							
	III									
July	I		-	-			-			
	III		-			**	-			
Aug	II		-	0		-	-		-	-
Sept	I			0			-			-
	II		-			-			-	
Oct	II		0						-	
Body weight										
June	II	-	-							
	III									
July	I		-	-			-			
	III	0	-			**	*			
Aug	II		-	-		-	-	-	-	-
Sept	I			-			-			-
	II		-			-			*	
Oct	II		-						-	

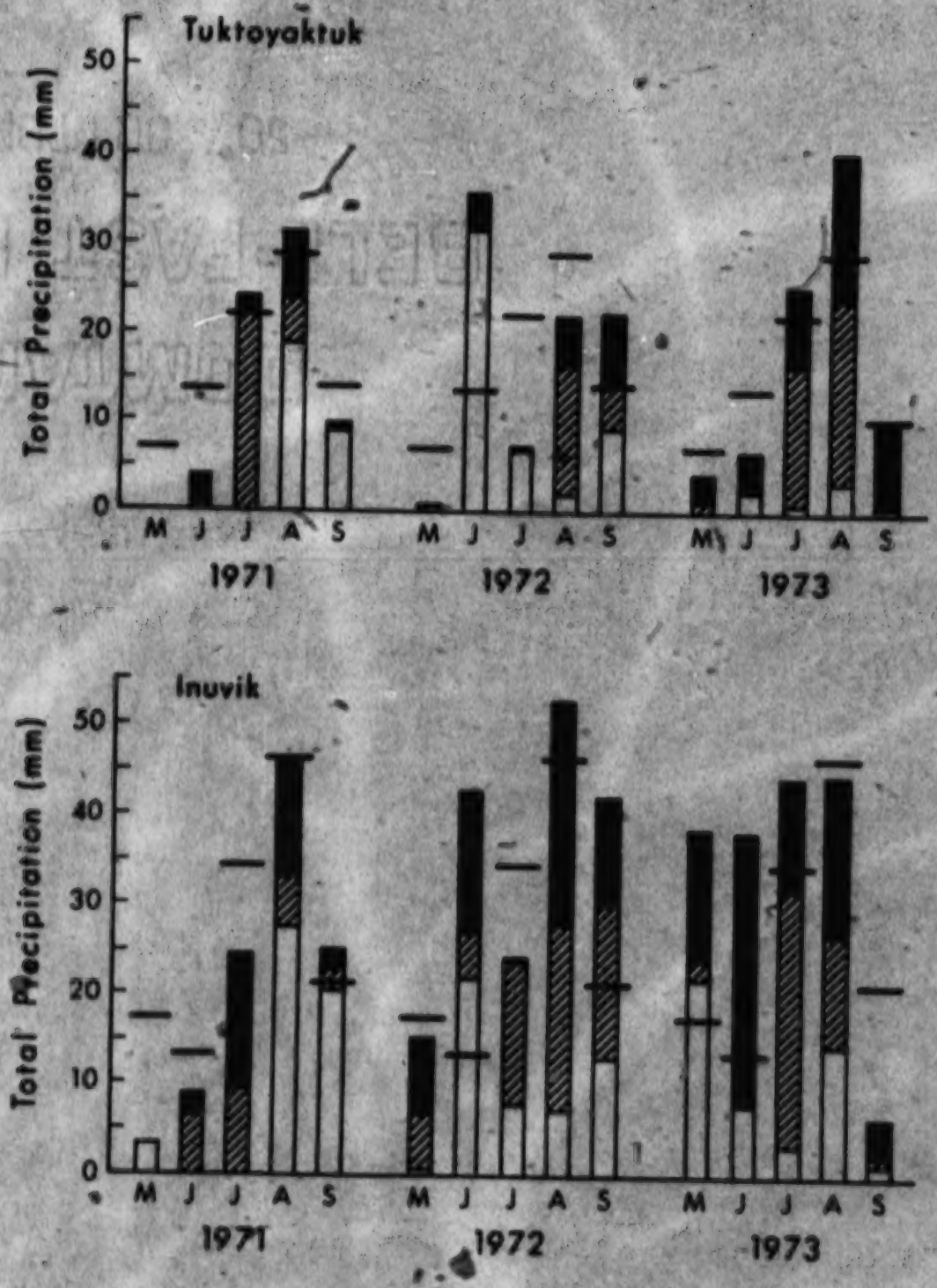
0 = could not be tested
- = not significant, $p > 0.05$
* = $0.05 > p > 0.1$
** = $0.01 > p > 0.001$
*** = $p < 0.001$



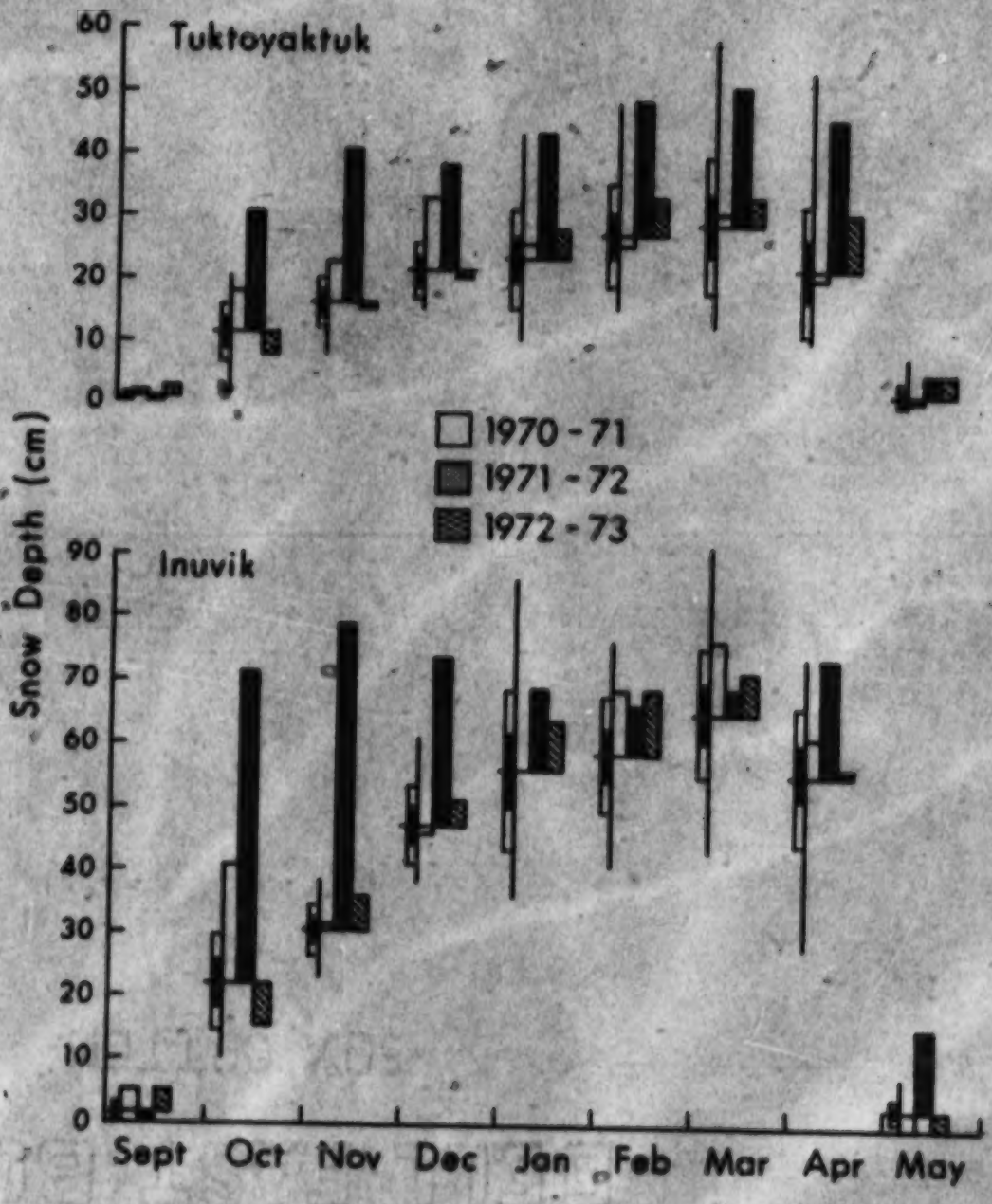
Appendix 20. Mean daily temperature (maximum and minimum), September-March by 10-day periods, at Inuvik and Tuktoyaktuk.



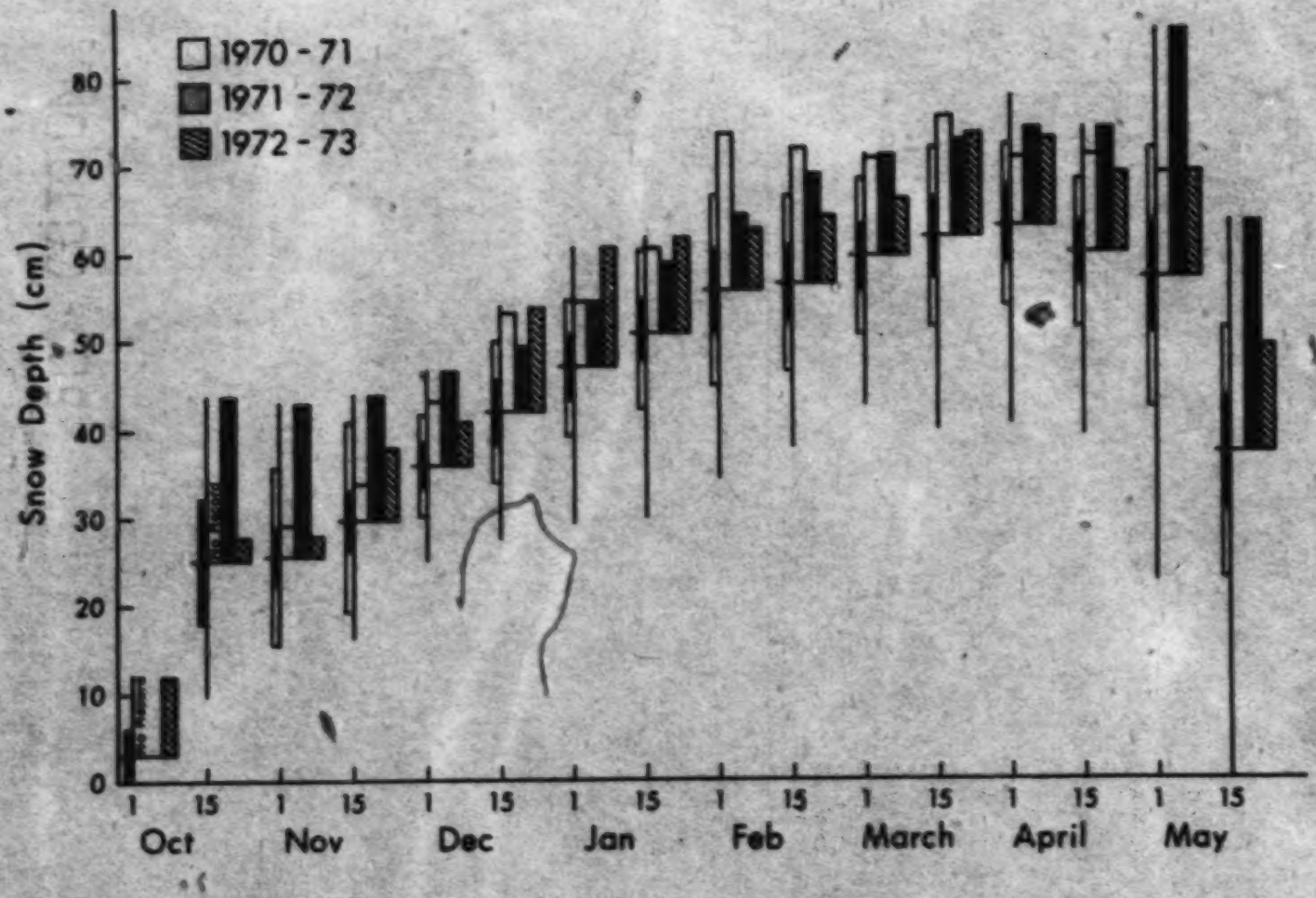
Appendix 21. Mean daily temperatures (maximum and minimum), April-September by 10-day periods, at Inuvik and Tuktoyaktuk.



Appendix 22. Total precipitation May-September by 10-day periods (1-10, open; 11-20, shaded; 21-end of month, solid) at Inuvik and Tuktoyaktuk. Normal monthly precipitation is shown as a bar.



Appendix 23. Snow on the ground at the end of the month at Inuvik and Tuktoyaktuk. The 1961-1970 mean ± SE ± 95% CL and range is shown to the left for each month.



Appendix 24. Snow depths at Inuvik (mean of 10 points) based on Environment Canada snow cover surveys. The 1965-1973 mean ± SE ± 95% CL and ranges are shown to the left for each sample.